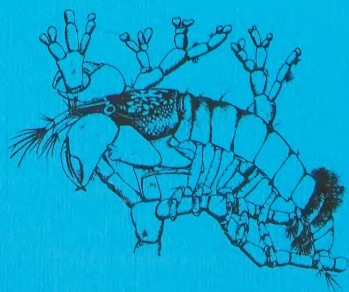


Functional Models, Life-History and Evolution of tube-dwelling Tanaidacea (Crustacea)

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FUNCTIONAL MODELS, LIFE-HISTORY AND EVOLUTION

OF TUBE-DWELLING TANAIIDACEA (CRUSTACEA)

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DISSERTATION

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LIST OF PAPERS

This thesis is based on the following papers, which will be referred to by their Roman numerals:

- I Johnson, S. B., Attramadal, Y. G. 1982. A functional-morphological model of *Tanais cavolinii* Milne-Edwards (Crustacea, Tanaidacea) adapted to a tubicolous life-strategy. Sarsia 67: 29-42. Reprinted by kind permission of Sarsia.
- II Johnson, S. B., Attramadal, Y. G. 1982. Reproductive behaviour and larval development of *Tanais cavolinii* Milne-Edwards (Crustacea, Tanaidacea). Manuscript. Mar. Biol. (Hamburg). Submitted.
- III Johnson, S. B. The reproductive strategy and dispersal of *Tanais cavolinii* Milne-Edwards (Crustacea, Tanaidacea). Manuscript.
- IV Johnson, S. B. A functional-morphological study of the tube-dwelling *Apseudes spinosus* M. Sars (Crustacea, Tanaidacea), and a comparison with deep-sea Tanaidacea). Manuscript.
- V Johnson, S. B., Attramadal, Y. G. 1982. A simple protective cod-end for recovering live specimens. J. exp. mar. Biol. Ecol. In press. Reprinted by kind permission of Managing Editor Margaret Barnes.
- VI Johnson, S. B. A functional-morphological model of tube-dwelling Tanaidacea (Crustacea). Manuscript.



INTRODUCTION

Tanaidacea is a well-defined order among peracaridan Crustaceans. However, its origin and phylogenetic affinity is more uncertain. The former name, Anisopoda, implies descent from Isopoda. In modern theory, e.g. Watling (1981), the Tanaidacea, together with the Cumacea, is considered to have a common ancestor with Spelaeogriphacea. The tanaids are cosmopolitically distributed having succeeded in colonizing environments from estuarine tide-pools and tropical sponges to the deep-sea down to depths exceeding 8000 m. Lately, interest for this group has increased as tanaids have been found to be widespread in the deep-sea of the great oceans in a previously unsuspected high abundance and diversity (Gardiner 1975). Fullgrown instars vary from 1.5 mm to over 25 mm, but most species of this order measure under 5 mm. Their small size and elongated body-form most likely contributed to the reason for the few records reported by earlier expeditions. This lack of information resulted in fragmentary species descriptions and a confused taxonomy which probably had the negative feed-back of hampering research in this group even in other disciplines.

In 1949, Karl Lang started his excellent work on the systematics and phylogeny of the Tanaidacea which provides the framework for most higher taxa today. The increasing records of deep-sea tanaids have been noted by Gardiner (1975) and Wolff (1956), who have described the occurrence of hermaphroditism and gigantism and further established their

world-wide and bathymetrical distribution. The main work concerning the anatomy of tanaids is based on *Tanais cavolinii* Milne-Edwards (Lauterbach 1970). Concerning embryology, *Heterotanaïs oerstedii* Krøyer was investigated by Scholl (1963). Other information on the biology of tanaids generally refers to a study by Bückle-Ramirez (1965). He described the life-history of the tube-dwelling *H. oerstedii*, its tube-building, reproductive behaviour and postmarsupial development, and suggested potential protogynic hermaphroditism in this species.

The fundamental concept of the interaction and affinity between structure and function remains diffuse. This is an important factor for a sound evaluation of taxonomical characters and an improved evolutionary approach to the systematics, and for an understanding of the ecology of this group, its role as a member of shallow water and deep-sea communities. For understanding the evolutionary processes which have taken place within higher taxa, the concept of functional-morphological models as put forward by Dahl (1976), has proved successful when tested on the Crustacea Malacostraca and on Amphipoda (Dahl 1976, 1977). According to Dahl, all functions should be taken into account for the model, but in practice, functional-morphological aspects are those most readily available. The morphological expressions for the mechanisms of locomotion, alimentation, respiration, reproduction, brood care etc. are to a higher or lesser degree interdependent and when considered together generally present a clear picture of the system as a whole.

FACTORS CONTRIBUTING TO THE CHOICE OF MATERIAL AND METHODS USED:

1) The French-Swedish ventures 'NORBI' and 'INCAL' gave me the opportunity of obtaining deep-sea material from the Norwegian Sea and the North Atlantic, two deep-sea areas separated by several ridges, and characterized by different fauna. No live material was obtained, and samples were preserved for structural analyses by means of SEM.

(Parts of papers IV and VI)

2) Functional studies on live material of the tanaids inhabiting the rocky tidal zone suggested the functional model. As an extreme example of adaptation of tanaids, the model was used as a valuable comparison. The study also followed the life-history for one year.

(Papers I, II, III)

3) Instead of studying exclusive deep-sea species, close relatives with a wide bathymetric range which are found elevated at high latitudes and in fiords, offer the possibility of obtaining live specimens for general comparisons.

(Papers IV, VI)

4) By improved techniques for recovery of live specimens and by the use of light-amplifiers, it was possible to study even deep-sea tanaids alive, obtained from the shallow arctic waters (500 m) of the Barents Sea during the 'marine benthos program (Norvarg) Ymer 80'.

(Papers V, VI)

SUMMARY AND CONCLUSIONS OF PAPERS INCLUDED IN THE THESIS

A FUNCTIONAL-MORPHOLOGICAL MODEL OF *TANAIS CAVOLINII* (I)

Rock-pools in the exposed tidal zone, which is the habitat of *T. cavolinii*, is an aberrant environment for species of Tanaidacea in general. Unlike members inhabiting or associated to soft sediments in shallow water or deep-sea, members of the family Tanaidae must be adapted to survive drastic fluctuations in turbulence, salinity, temperature and oxygen content. The confined, tube-living strategy of *T. cavolinii* which is reflected in its structural plan and life-history, has solved most of these problems. Food, consisting of various epiphytes and diatoms, is obtained from an area around the tube opening that can be reached without vacating the tube. The tube is made of exogenous fragments spun into a web together with mucous threads, released from the terminal dactyli of IIInd pereopods (spinning legs). Fecal products are fragmentized and incorporated in the inner tube wall, where bacteria and a microflora of diatoms develop. The spinning threads are also used as an anchoring life-line whenever moving outside the tube. This venture was only observed in copulatory males, but experiments revealed that the anchoring mechanism is developed in all instars. The physical properties of a tube have brought about several adaptations and functional solutions concerning the mechanics of locomotion. The elongated body-form, the differentiation of joints and articles, the distribution of spines and setae on the legs, and the short and stout antenna (AI, AII)

and uropods, are all functional expressions of limited tube space. The ultra-structures developed on the chelipeds and pereopods are functional devices for alimentation and cleaning. The reductions of the pleon, number of pleonites and pleopods (three well-developed pairs) are interrelated with the development of transverse bands of bristles on the first two pleonites. The importance of ventilating the tube, avoiding stagnant water conditions, has favoured a compact pumping mechanism to ensure optimal pumping efficiency. A prerequisite for this is a one-way water flow through the tube, made possible by the transverse bands, which when levelled with the pleopods prevent recirculation and minimize the leakage of water and hydrostatic pressure through the permeable tube wall. This explains the reductions in the posterior part of the pleon. This is the basis of a functional-morphological model with characteristics of the phyletic group, Tanaidae.

THE REPRODUCTIVE STRATEGY OF *T. CAVOLINII*, POSTMARSUPIAL DEVELOPMENT AND DISPERSAL (II, III)

The reproductive behaviour resembles that described in *Heterotanaïs oerstedii* by Bückle-Ramirez (1965). In *T. cavolinii*, living in strongly variable environment, the brood is protected by sealed off ovisacs, an aberrant form of marsupium. This species describes a unique form of parental care among invertebrates. Yolk is invested in the progeny in two phases, first in the eggs and later in the young. Facing uncertain

environmental conditions at the time of reproduction, the female minimizes reproductive costs by producing small eggs with a minimal amount of yolk. If, after fertilization, the brood fails to survive, the female can fall back on a new generation of eggs developing simultaneously in the ovaries. However, if the brood passes the 'critical stage', these eggs are transformed into yolk and sacrificed as food for the developing young. This two-phase nourishment strategy resembles Mammalia in that nourishment is supplied once for embryonal development, and again at a later stage to aid the development of viable young. This strategy complies with Mountford's 'bet-hedging' hypothesis (Mountford 1973), which stresses the importance of not only maximizing the number of offspring produced, but also of minimizing the probability of leaving no young at all. The impending risk of a complete or partial brood loss is counteracted by the female making the final energy investment when the young have passed the 'critical stage' in their embryonal development. The yolk-feeding results in larger larvae, which means increased survival capacity (Christiansen and Fenchel 1979).

Population structure and experimental studies of the post-marsupial development point to potential protogynic hermaphroditism as suggested for *H. oerstedii* by Bückle-Ramirez (1965). In unpredictable environments, where local populations (each rock-pool represents a local population) continuously risk extinction, survival of the total population is favoured by a strategy of potential protogynic hermaphroditism, which results in individuals with alternating sexes. This means

that all propagules of a new population may participate as females in the production of offspring and thus increase productivity rate and recolonization capability. In a system of rock-pools, isolated pools can be regarded as 'gene-banks' for the dispersed population, with genetic communication occurring frequently. Such a well-adapted, survival strategy in local habitats could be the key to understanding the world-wide distribution by passive drifting on tufts of algae (no pelagic larvae exist). By decreasing the risk of extinction in this way, the 'bet-hedging' principle is true at the population level as well.

A FUNCTIONAL STUDY OF *APSEUDES SPINOSUS*, AND A COMPARISON
WITH DEEP-SEA TANAIIDACEA (IV)

This study is based upon a functional analysis of the structural plan of *A. spinosus* with regard to ecological adaptations, and a comparison of these data with homologous structures in the deep-sea taxa, *Sphyrapus* and *Neotanaïs*. *Neotanaïs* has a cosmopolitan distribution in the deep-sea, excluding the Norwegian Sea and Arctic regions. *Apseudes* and *Sphyrapus* are characteristic inhabitants in deeper coastal waters, fiords and the deep-basins of the Norwegian Sea (*Sphyrapus serratus*). The functional model of *A. spinosus* corresponds to that of the tube-dwelling tanaid, *Tanaïs cavolinii* (paper I), with regard to joints and articles of the pereopods, and the location of spines and setae.

For *A. spinosus*, tunneling in the sediment involves the antennulae, chelipeds, IInd pereopods and all the other legs. Tunneling would not have been possible with only the 'fossorial limbs' (PII). Their stout bordering spines facilitate tunneling in mud intermingled with stones and gravel, and can therefore be regarded as an adaptation to this kind of sediment. Such sediments are common along the slopes in fiords and coastal waters, but unusual in the deep-sea, except for the Arctic where similar material is brought about by drifting ice. In *Neotanais*, the IInd pereopod is not so fossorially accentuated, usually having long bristles instead of stout spines. Yet this probably functions analogously in homogeneous, soft sediment. In the Antarctic or glacial areas of the North Atlantic, however, some species, e.g. *N. americanus*, *N. affinis* and *N. antarcticus* also possess stout spines on PII. Independent of whether spines or bristles are developed, their total fossorial area corresponds to that of *A. spinosus* and *Sphyrapus*.

The small rudimentary exopodites characteristic of monokonophoran tanaids and present in *A. spinosus* have a protective function and assist in respiration. In the dikonophoran, *Neotanais*, the elongated furrows on the carapace, which are respiratory pores, are protected exteriorly from fouling by a close lattice-work, and interiorly by the terminal brush of fine setae on the epipodite.

Pleopods are well-developed in both groups, not for swimming, but instead for ventilation and for assisting respiration by producing a one-way water-current through the tube.

Both *A. spinosus* and *Neotanaïs*, have homologous structures developed on pleon for sealing, preventing lateral and dorsal recirculation and thus increasing pumping efficiency.

The large amount of common characters within the two phylogenetic lines, Neotanaidae and Apseudidae, must have arisen through convergent and/or parallel development, as adaptations to similar abiotic environmental conditions, for tunneling and for tube-dwelling. Certain morphological differentiations are the result of differing kinds of substrates, which may also explain the diverging geographical distribution of these taxa. Evaluation of taxonomic characters should therefore be considered in the light of these factors.

A SIMPLE PROTECTIVE COD-END FOR RECOVERING LIVE SPECIMENS (V)

Benthic organisms in general, and stenotopic deep living species in particular, are sensitive to changes in environmental conditions and therefore must be protected from exposure to bathymetric fluctuations in salinity, temperature and light. Crustaceans subjected to the traditional recovery procedure have been noted to display abnormal behaviour. More fragile specimens suffer severe mechanical damage in unprotective cod-ends. A protective cod-end mainly for use on sledges is described for the recovery of living animal specimens independent of depth. It operates independently of surface signals. Mechanical damage of the specimens is avoided, as is exposure to bathymetric fluctuations of salinity,

temperature and light during recovery. The device has been tested on benthic and hyperbenthic fauna at varying depths down to 700 m. Specimens recovered and later kept in aquaria, had a low mortality rate compared with those sampled with ordinary cod-ends.

A FUNCTIONAL-MORPHOLOGICAL MODEL OF
TUBE-DWELLING TANAIIDACEA (VI)

The morphology of the body-form, legs and appendages in Tanaidacea is uniform, following a few general patterns which have been simplified into a tanaid model. The degree of abiotic impact on various structures in differing environments can be distinguished, and thus separated from or evaluated with characters of phylogenetic value. Most of tanaidacean taxa can be divided into two hypothetical guilds: tube-spinning forms and tube-tunneling forms. These can be further subdivided considering the nature of the tube, its permeability, and the substrate of the habitat. Finally, consideration should be taken to the animal's size. Most of the monokonophoran families and the dikonophoran neotanaids are tunnelers, while other taxa can be referred to as tube-spinners. Different taxa have acquired many morphological features in common, as a result of adaptation to a tube which is more or less circular in cross-section. The tube diameter is closely linked to the size of the body. The number of body somites is fixed and certain somites are

given priority, while others have been shortened to facilitate turning and locomotion. The cephalon segment is usually maximized, as well as the central pereonites 5-6 which give increased space for the development of eggs in the ovaries and larvae in the marsupium. All legs are developed for inverted (V-form) position. The dactyli of pereopods V-VII are developed as claws in species inhabiting tubes on hard-bottom substrates. In species dwelling in fine sediments, such as apseudids and neotanaids, the dactyli are developed as spines, often with setae arranged as ski-pole discs (paper IV). The pleopods are compactly developed and less natatorial (except for copulatory males) compared with other peracaridan crustaceans. The fringes of the pleopodal exopodites and their bristles are curved, following the tube wall. Each pleopod pair covers a semicircular area in the tube. The size, form, and number of pleonites, fusions or reductions, depend on the type of sealing arrangement, which is a consequence of the tube's permeability. Impermeable tubes are made by fine particles spun together, or by tunnels in fine sediments which are trampled and tightly packed. In smooth and regular tubes (spun or tunneled in fine sediment), the pereonites are smooth and dorsally curved in alliance with the tube wall to ensure their sealing function. Tubes which are tunneled in sediments intermingled with coarse material are winding with a varying diameter and irregular inner tube surface, which makes sealing more difficult. Sealing is thus improved by a narrow pleon with spiniform projections which are often

clothed with long, feathered setae. When embedded in mud, the pleon is enlarged, functioning as a soft seal.

Permeable tubes are prominent in the shallow-water family, Tanaidae. Tubes are spun on hard substrates, and are irregular with a varying diameter. Sealing is ensured by transverse bands of feathered bristles on the pleon. A reduced number of three pairs of pleopods is well levelled with the transverse seals for maximum pumping efficiency. Also, by being compactly positioned, they minimize the area of leakage along the tube wall. Complete lack of pleopods is a scattered phenomenon among different taxa, but distinguishes species of small size and/or narrow body-form, living interstitially or making tubes of larger particles. As leakage would be considerable, thus obstructing the through-flow of water inside a tube, pleopods are superfluous. Other phenomena influencing such small organisms are that the adhesion force of the water is comparatively increased. Further the viscosity increases when the temperature drops below 0°C , which is a common temperature in the habitats of several such species. This means that too much energy would be required to create a flow through the tube. An advantage is that respiration is facilitated by diffusion. Taken altogether, these factors may explain the reduction of pleopods in small and/or slender tanaids.

Analyses and comparisons of similar functional models constitute a promising approach to the problem of understanding the evolutionary processes which have taken place within higher taxa.

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A FUNCTIONAL-MORPHOLOGICAL MODEL OF *TANAIS CAVOLINII* MILNE-EDWARDS (CRUSTACEA, TANAIDACEA) ADAPTED TO A TUBICOLOUS LIFE-STRATEGY

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SARSIA



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The model is based on observations of living animals, functional analyses of structures, and in situ studies.

The body-form and differentiation of legs, articles, joints, and spines reflect locomotory adaptations to the tube. When moving outside the tube, a mucous thread released by the spinning legs (PII) acts as an anchoring life-line. The tube is built of various fragments and faeces, spun into a web as protection against predators, turbulence, UV-light, and desiccation. Three pairs of pleopods ventilate the tube by producing a posteriorly directed flow. When disturbed the flow can be reversed, as can the respiratory currents created by the epipodites. This, and the spine of the epipodite and the palpus of maxillulac, is a protection against fouling of 'branchial cavity'.

The food, dominated by epiphytic organisms, is scraped off by the chelipeds. Special structures are developed as cleaning devices.

Transverse bands of bristles on the pleon act as a seal, preventing backflow in an irregular tube. By reducing the size of the pleon and the number of pleonites, pleopods, and transverse bands, a compact pumping mechanism is achieved, minimizing water leakage through the tube wall in the pleopod area.

From this model morphological characters of the phyletic group Tanaidacea are presented.

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INTRODUCTION

The first study of a living tanaid was published by DENNEL in 1937. He described the feeding mechanism of *Apseudes talpa* (MONTAGU). This was the first attempt to make a functional-morphological analysis of a tanaid crustacean. In a study of *Heterotanaeis oerstedii* (KRØYER), FORSMAN (1956) presented protogynic hermaphroditism, which suggests a more complicated life history than was previously known. A more comprehensive investigation of the biology of *H. oerstedii* was presented by BÜCKLE-RAMIREZ (1965), who described tube-building, reproduction, postmarsupial development, etc.

Very little has been reported about the biology of tanaid crustaceans. Present knowledge on the functional morphology of tanaids is unsatisfactory, especially in the classification and ranking of taxonomic characters. The relation between higher taxa within Tanaidacea is therefore rather confused. New information concerning the interaction of structure and function is needed

to provide the basis for an improved understanding of the classification, and of the ecology and evolution of Tanaidacea.

The aim of our investigation has been to study the live, entire repertoire of the organism, *Tanais cavolinii* (MILNE-EDWARDS), with emphasis on the function of different structures resulting from ecological adaptations and evolution.

MATERIAL AND METHODS

Tanais cavolinii is abundant in the tidal zone along the rocky coast in the Bergen area, Norway.

Material was obtained from two different localities in this area; a sheltered tide pool in Raunefjorden at Ospøya, and a system of very exposed tidal pools on the islet Nord Oddane, situated west of the island Sotra (Institute of Marine Biology Reference numbers E 134–77 and E 12, 13, 41, 50–77 respectively).

The calcareous alga *Corallina officinalis* is characteristic of the tidal rock pools where it covers the bottom as a carpet of dense tufts. Among the basal branches of this alga, and in the crevices of the calcified bottom crust, *T. cavolinii* is present in great numbers throughout the year. During the

summer season the population density could be more than 10 000 ind. per m².

Samples were taken, twice a month throughout the year in 1977, from various parts of the tidal pools. Pieces of the bottom crust with *Corallina officinalis* were chopped out with a J-shaped scraper. Some of the material was immediately fixed in 4% neutralized formaldehyde, alcoholic Bouin, and 80% ethanol, for analysis of stomach content and the anatomy. Most of the material was kept in local sea-water and transported to the laboratory in thermal bottles.

Method of preparation for SEM

The method used here was reported in detail by NIELSEN & STRÖMBERG (1973) but the last phase in the dehydration procedure was slightly modified as follows: Abs. ethanol from 1:1 (2 changes), abs. ethanol from 1:2 (2 changes), and finally pure from (2 changes). The time between each change was about 20 min. Drying was done slowly at room temperature. The preparations were coated with gold palladium 2:3 and investigated by means of a Mark II Cambridge Stereoscan.

Methods for studying live animals

In the laboratory, animals were kept in circulating sea-water of about the same salinity and temperature as their natural habitat (32–34‰, 7–15°C). Some material with undamaged pieces of *C. officinalis* was transferred directly to the aquaria for studying the animals in their natural sites. The rest of the material was carefully fragmented and the tanaids were separated from the other fauna by means of a 2 mm sieve. A number of animals was transferred by a Pasteur pipette to Petri-dishes placed on a thermo-constant table. Sea-water, free of organic particles and rich in oxygen, was continuously circulating through the Petri-dishes.

Tanaid cavolinii is a tube-builder, and the wall of its tube prevents observation of its behaviour. The animals were therefore offered capillary glass-tubes of varying diameters corresponding to various instars. These substitutes were readily accepted. For observation purposes, a Wild M5 dissection microscope, movable in all directions above the aquaria and Petri-dishes, was used. Although the eyes of *T. cavolinii* are poorly developed (ANDERSSON & al. 1978), the animals reacted to sudden changes in light intensity by avoiding the light from the microscope-lamp. The animals were therefore slowly adapted to light of approximate daylight intensity which was kept constant during the daytime. For this purpose, a 150 W daylight lamp was used at a distance of about one meter. An effect of the increased light was that the growth of the microflora on the substrate was continued. Under these circumstances, a large number of individuals could be kept alive for months and even raise healthy broods.

To detect water currents inside the tube, suspensions were released close to the tube openings. The suspensions used were: sea-water with natural particles such as unicellular algae, sea-water with detritus, and occasionally, a weak suspension of sea-water and Carmine-red.

RESULTS

The following phenomena of the live animal were studied: walking, locomotionary adaptations, tube building, feeding, the respiratory mechanism, the pleopod pumping mechanism, and cleaning.

Walking

Of the six pairs of pereopods (P11–P17) only P11, the spinning legs, are not involved in the walking procedure. The other legs are strongly and uniformly developed. The pereopods can only be extended to a maximum angle of 120° (Fig. 1), because the way in which they are suspended, between the basis and coxa, limits movement. The first three pairs of pereopods, P11–P14, are hinged to the coxa at two points, and so can swing in a straight line anteriorly and posteriorly but only slightly lateromedially. The subsequent three pairs of legs have their basis hinged to the coxa at only one point. This enables them to move more freely in all directions, and to be almost straight when extended. The other articles of the pereopod are hinged at two points, so their movement is restricted. As the article ischium is missing, the basis is instead articulated with the merus. This limits the bending of these articles to an angle of appr. 30°–120° of each other (Fig. 1). The propodus and the dactylus constitute the functional 'hand', which keeps in contact with the substrate. The pereopods can never be extended more than the figure shows. This means that they are too short to reach a flat surface and still function well as walking limbs.

Locomotionary adaptations outside the tube: the anchor line

The first pair of legs (P11) is characterized by a more slender shape and a prolonged dactylus (Figs 2, 3). Situated on the distal part of the spiniform dactylus, is a subterminal pore (Plate 1A), which releases the very thin spinning thread. This thread plays an important role in acting as a life-line for the animal when moving in exposed habitat. In this way, the animal attaches itself safely to the substrate. It is almost impossible to wash it away even from the smooth surface of a nylon bucket. As the spinning thread is invisible to the naked eye, this anchoring procedure is only revealed by the incessant movement of the spinning legs. As the spinning legs are continuously occupied

with the anchoring procedure, forward movement is mainly effected by the chelipeds with which the animal can climb from one branch to another gripping, dragging, and bending the calcified branches. The pereopods are also more efficient climbing among branches of algae (Fig. 4) than walking on flat surfaces. Climbing is a slow procedure, however, and although the life line may secure the animal from being washed away by wave turbulence, such an openly exposed animal is easy prey to predators. During the summer season, we repeatedly observed climbing copulatory males being attacked and eaten by the isopod *Idothea pelagica* LEACH. No defensive behavior was noted. The well-developed chelipeds seemed to be of no use in defence against the predator. Walking or climbing outside the tube is a rather rare event restricted to copulatory males in the spring and summer season. Other instars are confined to their tubes and immediate surroundings.

T. cavolinii is also able to swim to a very limited extent. By forceful, synchronous strokes of the pleopods, it can swim for a few seconds forwards or backwards in small jerks. This occurs if the animal is disturbed or released in the free water column. Alternately, it could contract into a ball and sink passively to the bottom.

Locomotionary adaptations inside the tube

Locomotion is much improved inside the tube because the pereopods PIII–PVII can work in their natural 'inverted' V-form position (Figs 3, 5, 6). Developments such as the differentiation of articles, joint-angles, and the distribution of the spines and setae of the legs, are adaptations for improved locomotion inside the tube. The V-form position and good contact with the tube wall allow rapid forward and backward movements. The large chelipeds are kept close to the sides of the carapace lobes and are not used for locomotion. The spinning legs (PII), carried medioventrally, are not used for anchoring but for spinning and maintaining the tube-network. The ability to turn inside the tube is a prerequisite for spinning. Turning is attained by ventral bending of the body, and is sometimes facilitated by the flexibility of the tube wall. The three pairs of pleopods do not have any locomotory function inside the tube. Their main function is to create a water current through the tube. The short and stout antennae (AI, AII) and uropods are well balanced for tubi-



Fig. 1. Caudal view of pereopod IV showing the angle between the basis and merus-carpus, extended to the maximum (120°) and folded to the minimum (30°).

colous locomotion. Their armament of bristles and setae, in contact with the tube wall, function as tactile sense organs both inside the tube and when postured at the front opening (Fig. 3B).

Tube building

The tube material

The tube is built of material available in the surroundings. The outer surface of the tube



Fig. 2. Maxillulae with articulated palpus (above). The spinning legs PII, left (middle) and right (below), with the ischium article missing. (Scale mark 0.1 mm.)

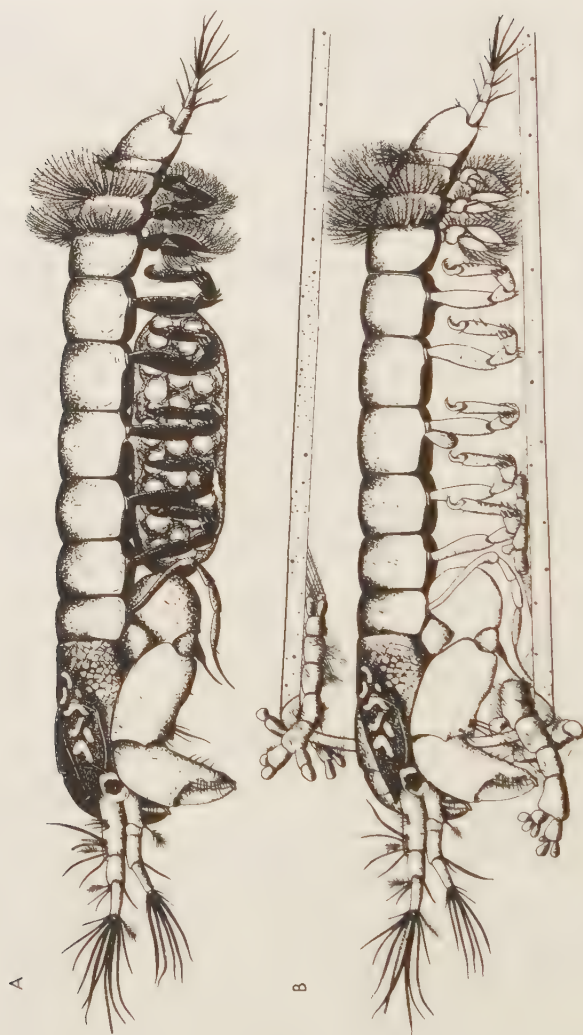


Fig. 3. A. Copulatory female with ovisacs and eggs. B. Female with rudimentary oostegites, postured at the front opening of a capillary glass tube. Note the position of the chelipeds and spinning legs, the inverted position of pereopods III-VII, and the levelled position of the pleopodal bristles and the pleonal transverse bands ($\times 24$).



Fig. 4. Copulatory male climbing among branches of *C. officinalis*. Note the heavy pigmentation of the carapace and the antennulae, the sexual dimorphism of the chelipeds, the anchoring procedure of the spinning legs, and the holding function of pereopods PIII–PVII.

consists mainly of fragments of *Corallina*, bivalve shells, grains, etc. The inside is covered with fecal products spun into the web together with old cuticular remains. The chelipeds frequently fragmentize pieces of algae to use as building bricks for the tube. Sedimented small particles are scarce in the exposed habitat. Smaller remains after a meal are often used immediately as reinforcements. Larger pieces are utilized for elongation of the tube front. Tubes in the lower tidal zone are strongly armed and well camouflaged by the living algae surrounding them. In the uppermost tidal zone, most exposed to drainage, the tubes are not hidden or sheltered by a carpet of algae, but instead have a higher content of fecal products which colour the tube wall grey and give it a thick and porous structure. During drainage the water inside the tubes is retained.

The spinning procedure

The tube construction is the result of coordination between the spinning legs and the chelipeds, often assisted by the palps of the maxillipeds. The chelipeds prepare a piece of building material and put it into place. It is secured by the spinning threads from the dactylus pores, which press against it for a short moment, and then move on to the next piece of material and so on in quick alternating movements. The spinning pattern is not random. To ensure optimal function and strength the mucous threads need to be orientated so that the fibre layer can serve as a framework for keeping the pieces together. The spinning procedure involves a very slow movement, anterior or posterior, with a simultaneous slight rotation of the body around its longitudinal axis. This procedure is not absolutely strict, but the spinning pattern of the threads generally follows the sequence



Fig. 5. Caudal view of a cross-sectioned tube. Note the functional location of spines and the inverted position of the legs. The semicircular transverse band of feathered bristles is well integrated with the bristles of the pleopods, allowing only a ventral flow.

described in Fig. 7. The alternating positions of the two spinning legs are marked in the figure by the circles 1-3. Each circle indicates the approximate spot where the threads are cemented. Each spinning leg generally connects

the spots 1, 2, and 3 on its own side, but there is an overlapping area within the dotted lines between spots 1 and 3 where both legs cement their spinning threads. When one leg is in position 2, the other leg is in position 1 or 3. The threads orientated in this way overlap in four main directions (Fig. 7, below). With an angle of approximately 45° between the main directions, the net is presumably strong in all directions. After some layers of reinforcing threads have been added, the tube wall becomes a strong and flexible network. The ultrastructure, seen on a SEM-micrograph (Plate 1B), recalls the ultrastructure of fine filterpaper.

The tube of *T. cavolinii* is more or less continuously added onto at the front end. It does not grow in any special direction, but it is influenced by the substrate topography, crevices, etc. The length of a tube may therefore vary considerably, but is generally limited to about four or five times the length of the body, which makes the average tube about 20-30 mm long. As the posterior end of the tube is firmly closed, the water current created by the pleopods, must be continuously pressed out through the wall network. Probably, the organic matter from fecal products and the water circulation encourages the development of a rich microflora



Fig. 6. Pereopod V of preparatory female.

The differentiation of articles and joints and the location of tactile setae and cuticular spines constitute a functional-morphological plan developed for optimal locomotion in a tube.

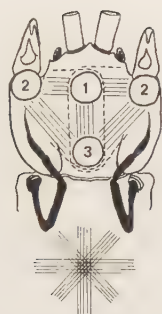


Fig. 7. Diagram of the ventral cephalon view, illustrating the spinning sequence. The spinning legs are indicated in solid black. The circles indicate the general spots where the mucous threads are cemented to form the web. — Below: direction of spinning threads.

of diatoms on the inner tube-surface (Plate 1B). This feature was typical for tubes belonging to copulatory females. Tubes of copulatory males were less developed and less well maintained. They were often shorter, open at both ends, and constructed more simply. Diatoms were never abundant in tubes belonging to copulatory males.

Feeding

Stomach content analysis

About 50 animals of varying instars were collected at daytime and fixed immediately. Stomachs and intestines seemed to be well filled with a homogeneous mass of fragments of microscopic epiphytes and pennatulate diatoms. No animal remains were identified. We cannot, however, exclude the possibility of a differing nutritional activity during the night.

The feeding procedure

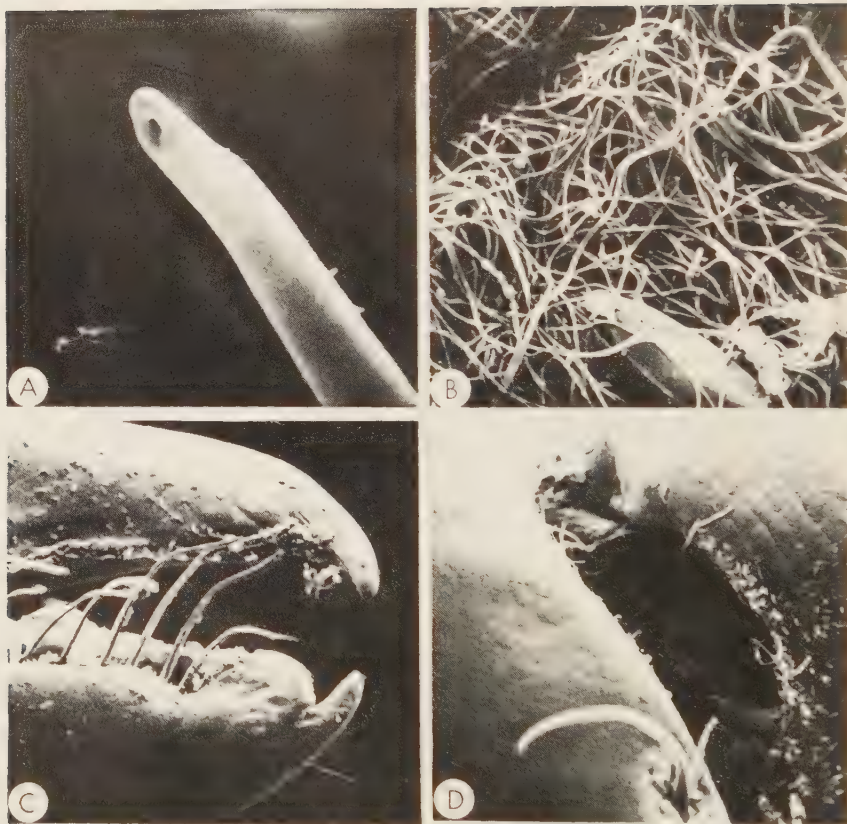
The stomach content confirmed our observations of the feeding behaviour. Feeding is a lengthy procedure, taking place at the front-opening of the tube and its immediate surroundings. *T. cavolinii* uses its chelipeds to cut off small pieces of algae or scrape the epiphytes off *C. officinalis* and other surfaces. The chela has a medial row of small, stout setae close to the edge of the propodus (Plate 1C), which serve as collectors, and



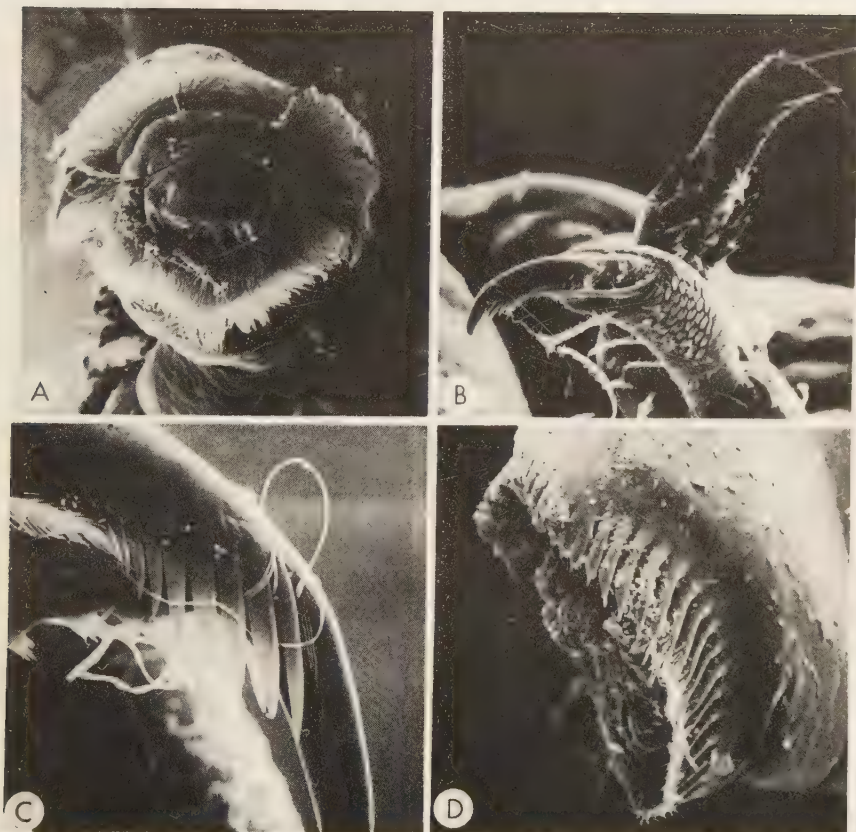
Fig. 8. The maxillipedal epipodite with the distal spine above.

conveyors of smaller food particles to the mouthparts. The chelipeds are also skilfully used as a pair of tweezers for grasping selected pickings. The maxillipeds have extended palps, the setae of which form a basket, collecting the food by combing it off the chelipeds. The food is then treated by the mouthparts and finally conveyed to the stomodeum and the chewing stomach. Larger pieces of algae could serve as a food supply for a longer period. In some cases, a smaller branch of *C. officinalis* was dragged inside the tube and consumed within a few days. This might be a way of satisfying calcium-needs. The chelipeds and the cephalothorax are heavily calcified.

The animal very seldom vacates the tube. The dactyli-claws of the last pair of legs (PVII) are usually safely hooked inside the tube-front, ready for immediate retreat. The tubicolous food-strategy described above makes the species dependent on the productivity of a very restricted area, but we have not found any obvious connection between a low food supply and migra-



A. Distal part of the dactylus on the spinning leg showing the pore from which the mucous thread is released ($\times 2400$). B. Ultra-structure of the network of the interior of the tube wall. A pennatulate diatom is seen in the lower part ($\times 2400$). C. Distal part of the cheliped showing the sharp edges, the alimentary setae, and the distal aperture ($\times 380$). D. The right respiratory pore at the posterior margin of the carapace ($\times 600$).



A. Caudal view of the pleon showing the circular connection between the transverse bands of bristles on the pleon and the bristles on the pleopods ($\times 60$). B. The propodus and dactylus of pereopod VI (left) and pereopod IV showing the ultrastructural cleaning devices of the cuticle ($\times 240$). C. The cuticular cleaning combs situated medially on both sides of the dactylus on PVII. Note the thin spinning thread ($\times 1200$). D. The processus molaris on the mandibulae of a copulatory male ($\times 840$).



Fig. 9. A. Schematic drawing of the water currents that normally flow through the carapace lobes and through the tube. The respiratory water enters through the dorsal respiratory pores when the ventilatory current is posteriorly directed. B. Retreated position at the posterior end of the tube, illustrating the reversal of the water current by both the pleopods and the epipodites as a reaction to the presence of foreign matter.

tion. Although the food supply was kept purposely low in some aquaria, the animals seldom departed from their tubes. In their natural habitat they appear to have the same food-

strategy and the same partly scraped areas around the tube openings. In order to reach a more favourable area, they elongate the tube with additional material.



Fig. 10. Dorsal view of the carapace showing the strong, blotched pigmentation. Scale mark 0.1 mm.

Respiration

The epipodite pumping mechanism

The morphology of the respiratory organ has been described by LAUTERBACH (1970). The inner surface of the two lateral carapace lobes is coated by vascularized tissue with respiratory function. Inside each lobe a maxillipedal epipodite is responsible for creating the respiratory water current through the cavity (Figs 8, 9). The epipodite also has respiratory tissue, but additional respiratory organs are unknown within Tanaidacea. According to LAUTERBACH (1970), the respiratory current in *T. cavolinii* flows in the opposite direction to the current in *Herpotanais* (Neotanaidace) and *Leptochelia* (Paratanaidace). The two dorsal respiratory pores at the posterior edge of the carapace valves (Fig. 10, Plate 1D) serve as outlets for the respiratory current. The intake is through the ventral pores.

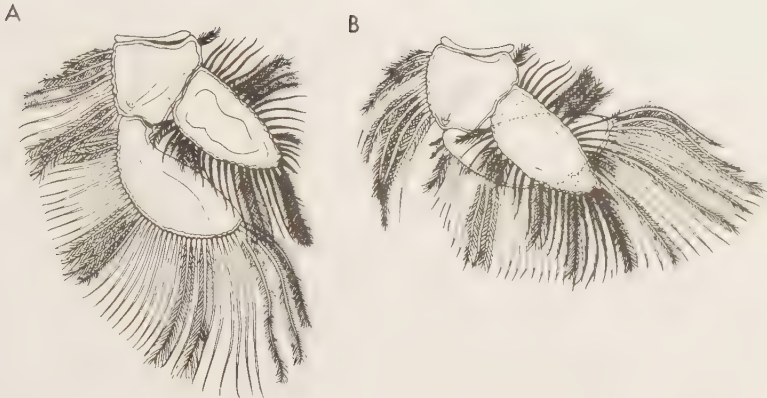


Fig. 11. Caudal view of the left pleopod ($\times 125$). A. The pleopod spread out like a fan during the power-stroke. B. The pleopod in folded position when retreating or resting. The exopod overlaps the endopod rostrally.

LAUTERBACH suggests that this is an adaptation for tube-dwellers. GAMBLE (1970a) found that for *T. chevreuxi* DOLLFUS, only the pumping frequency of the epipodites responded to low O_2 concentrations. The carapace lobes are therefore probably the only respiratory organ. He also noted that *T. chevreuxi* survives well under anaerobic conditions (depending on temperature), and regards this as an adaptation to a tubicolous and sessile life (GAMBLE 1970b). According to our observations, epipodites normally create a water current through each 'branchial cavity' in the direction illustrated in Fig. 9A. The respiratory water enters through the dorsal pore and leaves through the ventral pore, close to the base of the maxillipeds. The pumping of the two epipodites is always synchronized, but the frequency can vary considerably from 0.5 to 3 beats per second. Water currents around the body are shown in Fig. 9A. Normally the posteriorly directed water current generated by the pleopods, passes under the ventral pores. This water flow generates a vertical sub-pressure gradient in the tube. The epipodite works the easiest way, pumping the water along this gradient. Thus, respiratory water is taken in dorsally and expelled ventrally.

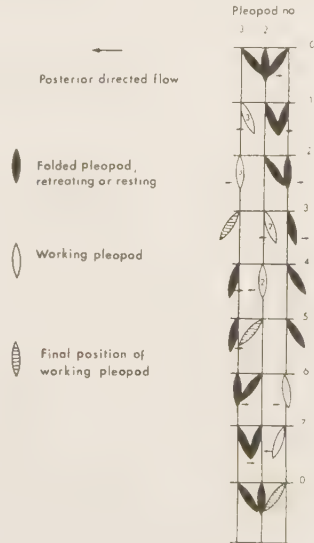


Fig. 12. The metachronal rhythm and stroke amplitude of the pleopods. 0-7 describes the sequential movement of the pleopods.

The pleopod pumping mechanism

When the three pairs of pleopods are working, the exopods and endopods are spread out like fans during the power-stroke and are kept folded during the retreat (Fig. 11A, B). The pleopods work in a metachronal rhythm, which means that the water current is not in constant flow because there is a short break between two sequences, when the pleopods are in resting position (Fig. 12). The duration of a sequence normally varies from 0.2–1.5 seconds, while the frequency can vary from 3 per second to zero. As is noted by GAMBLE (1970a), the pumping activity can be stopped for several minutes. When spinning or walking, the pleopods are usually folded in the resting position (0 in Fig. 12) and the pumping activity is intermittent. The posterior direction of the pleopodal power-stroke and the water current is only true for undisturbed animals, as the direction can be reversed under disturbance of any kind. For example, when a suspension of Carmine-red was released close to the tube opening, the reaction was an immediate retreat to the innermost end of the tube (Fig. 9B). Simultaneously, more agitated, anteriorly-directed pumping began, expelling the suspension. If conditions get worsened, or when an intruding neighbour appeared at the tube opening, the defender made very powerful water blows with synchronous strokes of the pleopods.

A feature of *T. cavolinii* important for the pumping mechanism is the transverse bands of feathered bristles occurring on the pleon. These are situated on the posterior margin of the first two pleonites (Figs 3, 9). Together with the pleopods they form an almost circular border of bristles around the body (Fig. 5, Plate 2A). When pressed against the tube wall dorso-laterally, the bands of bristles act as an efficient seal, preventing water from recirculating. The ventral one-way water current must thus be pressed out through the tube wall. This means that the posterior part of the tube acts as a filter, collecting small particles and organisms (diatoms) on the fine-meshed inner surface (Fig. 9A, Plate 1B). The adults were never seen feeding on this microflora, but the manca larvae released in the tube used it as a first source of food. The pleopod pumping mechanism might therefore be an important means of supplying food for the mancas.

GAMBLE (1970a) also tested the response of

the pumping frequency to low oxygen concentrations. The pleopod pumping did not change significantly with changing concentrations and there is nothing else that indicates that the pleopods of tanaids have any direct respiratory function.

Reversed currents – a linkage between the pleopods and the epipodites

Although the pleopods and epipodites work independently, there is a linkage between the direction of the pleopodal current and the respiratory current. When the pleopodal current is posteriorly directed, the respiratory currents pass through the 'branchial cavity' from the dorsal to the ventral pores, as mentioned above. But when the pleopod-pumping is reversed, the epipodites also simultaneously reverse the respiratory flow (Fig. 9B'). Though the pressure gradient changes in this manner, the vital reason for reversing the respiratory current is to protect the respiratory pores and the 'branchial cavity' from being clogged by foreign particles in suspension. The well developed spine on the distal part of the epipodite (Fig. 8) has the probable function of protecting and cleaning the dorsal respiratory pores. Analogously, the palpus of the maxillulae may serve as a cleaning device to keep the ventral pore open (Fig. 2). LAUTERBACH (1970) used several kinds of dyes to trace the respiratory currents of *T. cavolinii*. We tested some suspensions of Carmine-red, Indian-ink, and Methylene-blue on animals, both in tubes and unprotected in Petri-dishes. The epipodites and pleopods immediately reversed pumping. Such occasional observations must therefore have little relevance as a means of recognizing phylogenetic kinship.

Cleaning

Specially developed cleaning devices

Special structures have been developed as cleaning devices to prevent infesting epizoids from settling and to keep vital appendages and setae from fouling (See Table 1). On the chelipeds, the sharp edges of the dactylus and propodus and the row of small setae (Plate 1C) serve in alimentation and also in the cleaning of the antennulae and antennae, which have important sensory functions. The antennulae and antennae are cleaned by bending ventrally and being

drawn through the slightly open chela. When the chela is closed, a tiny aperture appears distally between the 'finger' and the dactylus (Plate 1C). The delicate dactylus spine of the spinning leg (PII) can be pulled through this aperture in order to release lumps of mucous threads. On pereopods PIII-PVII, the sternal and tergal sides of the distal articles are provided with striated cuticular scales (Plate 2B), which have their cleaning function in scratching the neighbouring legs. Consequently, the epizoics attach themselves to the caudal and rostral sides of the legs, especially on the basis article. Settling on these areas might also be favoured by water currents that are canalized between the basal parts of the legs. The dactyli of pereopods PV-PVII have distally, on both sides, well developed cuticular serrations (Plate 2C). The flexible basal joint of these posterior legs allows for a wider action radius. These cuticular combs clean the neighbour pereopods and the feathered bristles of the pleopods. The uropods are often cleaned at the same time by bending ventrally.

Moulting

Most instars were richly infested with stalked ciliates of the order Chonotrichida, which are well known for their affiliation with crustaceans (MOHR 1959). The ciliates prefer to settle on places exposed to water currents, from which they probably feed. They became red after being exposed for only a few minutes to a Carmine-red suspension. Settling areas beyond cleaning-reach are: the oral parts, the basis of the legs, and the bands of bristles on the pleon. To some extent the oostegites were infested, but as these tissues are very thin and weak, and cleaning exposes them to hazards, their only form of 'cleaning' is the high frequency of moults that precedes the copulatory stage. The moulting procedure of *T. cavolinii* is about the same as described for *Heterotanaos oerstedii* by BÜCKLE-RAMIREZ (1965) and by FORSMAN (1956), with the exception that *T. cavolinii* was never observed moulting outside its tube. To moult in an exposed position must put the animal in great peril. According to our observations, the moulting always took place inside the tube, and the exuvie was thereafter generally used as tube reinforcement. In the middle of the moulting procedure, infested stalked ciliates released themselves from the old cuticula and swarmed around

Table I. Cleaning and cleaning devices.

Structures cleaned	Cleaning devices used
Antennulae & antennae	Chelipeds (with maxillipedal assistance)
Chelipeds	Other chela (with maxillipedal assistance)
Spinning leg (PII)	Chela, distal aperture (with maxillipedal assistance)
Pereopods (PII-PVII)	Neighbour pereopods
Pleopods & uropods	Pereopods (PVI-PVII)

until the animal finished moulting and was lying quiet and immobile, unable to prevent their resettlement. The new settlers were only about half the original number, but were attached in the same strategical positions as before. The remaining epizoics on the exuvie were later eaten.

A species of harpacticoid copepods (Tisbidae), that was regularly seen inhabiting the tube may also have a cleaning function. The harpacticoids seemed to be feeding very actively from the inner tube surface and also from the smaller epizoics on the host. It is possible that the harpacticoids stay and even reproduce inside the tube.

DISCUSSION

Rock pools in the tidal zone are exposed to great variations of environmental factors such as: salinity, temperature, and turbulence, caused by rain, wave-action, and draining. Therefore all inhabitants must be adapted to survive drastic fluctuations. In this habitat the dense carpets of *C. officinalis* covering the calcified bottom-crust, serve both as a substrate for different kinds of epiphytes and as protection for a rich fauna. Non-sessile organisms such as many crustaceans, must be good clingers to escape being washed away.

The tube-living strategy of *T. cavolinii* solves this problem. But the evolution of this way of life has given rise to new problems and solutions, many of which are reflected in the functional morphology and the life history. The physical properties of a tube have brought about several adaptations and functional solutions in the mechanics of locomotion, alimentation, respiration, etc. The elongated body-form, the differentiation of joints and articles, the distribution of

spines and setae on the legs, and the short and stout antennae (AI, AII) and uropods, are all functional expressions of limited tube-space. The central suspension of the posterior legs PV–PVII allows for a wider action radius, which may reflect the importance of flexible cleaning devices. The chelipeds are used for locomotion outside the tube, but their main function is alimentation and tube-building. They may seem large in comparison with other dikönophorans (*Typhlotanais*, *Leptognathia*, *Leptochelia*, *Paratanais*, *Neotanais*, etc.), but because of their compact construction and their position in close contact with the carapace, minimal space is required.

The fact that the ischium article is missing exclusively in the pereopods of Tanaidae is remarkable. Possibly the stability of the inverted V-form position of the legs is improved. Other tube-dwelling tanaisids (e.g. *Typhlotanais*, *Leptognathia*), have developed shorter and stouter legs, but show no reductions of this ischium article. The slender spinning legs (PII) deviate from the other more uniform pereopods. The first three pairs of pereopods of other dikönophorans (except *Pseudotanais*), are generally slender and uniform but whether they all have a spinning function is unknown (except for *H. oerstedii*, BÜCKLE-RAMIREZ 1965).

The anchoring behaviour of *T. cavolinii*, using a life-line whenever moving in the habitat, is a notable mechanism for a crustacean. Such a mechanism must have evolved in a habitat featured by turbulence, and an absence of fine bottom sediment, which would be fatal as fine particles together with mucous threads would soon immobilize the animal. The fact that all instars, not only copulatory males, have this anchoring behaviour indicates the importance of the life-line when moving outside the tube.

The restrictions of an almost sessile tubicolous life-strategy are credited by several advantages of the tube itself. A tube gives protection from many aspects. As a security against predators, a tube associated with *C. officinalis* is usually unapproachable, being well armed with calcareous fragments. When a tube is not associated with algae, the amount of incorporated fecal matter is increased. This matter resembles the surroundings and acts as a camouflage. As a refuge during the ecdysis and the postmarsupial development of the first manca stages, the tube is a defensive structure of vital importance. The declining degree of pigmentation from the carapace to the pleon is probably correlated to

the degree of light exposure. As the posterior part of the body seldom vacates the tube, the pleon is seldom directly exposed. Although the cephalothorax is strongly pigmented (Figs 3, 10), the tube may offer sufficient protection against too intense UV light. For the population living in the uppermost tidal zone, lacking sheltering algae and thereby exposing their tubes to sun and wind, the greatest danger is desiccation and overheating. But the thick and porous tube wall might be protection against this. During drainage, water remains inside the tube owing to the capillary force, but this very small volume would soon be overheated if not protected from direct sunlight. The porous structure allows for some evaporation, which may have a cooling effect, but mainly seems to prevent complete desiccation.

A tube may be favourable for screening off the surroundings and isolating the inner environment, but at the same time, it might create stagnant water conditions, especially when closed at one end. This must be avoided either by an active transport of water, or by exposing the respiratory organ to oxygenated water outside the tube.

As the respiratory tissue is located in the carapace as stated by LAUTERBACH (1970) and GAMBLE (1970a), the pleopods must have some other function. LAUTERBACH (1970) refers to *T. cavolinii* as a potential filter-feeder, but this is not possible as no filtering devices are present. The maxillipeds are too small to cover even the ventral tube opening, and filtering setae are lacking. The quantity of water pumped through the tube is also insignificant. As a comparison, we have studied the filter-feeding amphipod *Erichthonius difformis* (MILNE-EDWARDS), a tube-dweller of about the same size as *T. cavolinii*. This amphipod has well developed filtering setae and a several times larger waterflow through its tube. *T. cavolinii* has carapace-respiration and is not a filter-feeder. Despite this, pleopods are well developed, though reduced in number.

The pumping frequency of the pleopods is not correlated with variations in oxygen supply, as is the pumping of the epipodite (GAMBLE 1970a), but this does not necessarily prove that the pleopods are unimportant for respiration. The respiratory current of the carapace is too weak to create sufficient ventilation of the tube. The pleopods, however, are sufficiently well developed to prevent stagnant conditions. They might also be of vital importance to the oxygen

supply of eggs and embryos in the marsupium, and to the newly hatched manca larvae. The microflora on the inner tube wall would also be favoured. Without pleopod pumping, it would have been impossible to ventilate the tube enough to ensure brood-survival etc.

Other aspects to be mentioned, though no conclusions are drawn, are: the chemosensory communication by means of the aesthetascs on the antennulae, the reversed pumping against intruders or foreign matter, and the filtering role of the posterior part of the tube.

The importance and function of the pleopods as a ventilatory mechanism is clear, but the structural interrelationships of the reduced pleon and the transverse bands are more complicated. Due to the uneven substrate of the habitat, the tube often becomes irregular and varying in diameter. To facilitate a one-way flow through such a tube, the transverse bands on the pleon act as a 'seal', preventing backflow of water in the tube. This can only be achieved if the fringe of bristles on the pleopod is levelled with the transverse band of bristles, thus forming a water-tight 'seal' to prevent backflow. If this close contact is lost, the ability to produce a one-way flow is also lost. The regular spacing of the pleopods is likely to ensure optimal pumping efficiency. Obviously, there must be a minimum working distance between the pleopods, depending on the amplitude of the stroke. If the distance between two pleopods is too great the continuity of the metachronal flow will be lost, because this would mean there would be a gap between the power-stroke of one pleopod and the next. For metachronal pumping, the minimum number of pleopods is two pairs. Tanaiids generally possess five pairs, or have no pleopods at all. If *T. cavolinii* had retained all pleopods (with no reduction of pleonites), extra bands of bristles would have been needed, one band for each pleopod pair. This would result in a much longer pleon, but five different bands would not be a more effective 'seal' because of the irregular diameters of the tube. A leakage in one of the five potential 'seals' would be enough to reduce the effectiveness of the co-operating pleopods.

Perhaps more important is that the tube wall is a network permeable to water. The water flow produced is based on the hydrostatic pressure gradient that is generated by the pumping. A leakage through the network in the pleopod pumping area would result in a de-

crease in the hydrostatic pressure and a consequent reduction in pumping efficiency. Therefore, the pleopod area of the tube wall, where this pressure is generated, should be as small as possible to minimize leakage. This means that a efficient pumping mechanism favours a smaller pleon, and a reduced number of pleopods, pleonites, and transverse bands. The anterior part of the pleon is most easily maneuvered into the sealing position because of its proximity to the pereon, and more particularly to the pereopods. This explains the reductions in the posterior part of the pleon.

The above mentioned structural specializations reflect this species' confinement to an algae-associated rocky habitat, and its exclusive occurrence in the tidal zone. This places *T. cavolinii* and its few phyletic relatives in an isolated position at an evolutionary 'dead end' among the dikionophoran tanaiids.

Unreduced mouthparts (e.g. the mandibulae, Plate 2D) of copulatory males are found only among Tanaiidae. Whether this is a primitive character or not is uncertain. From a functional-morphological model of *T. cavolinii*, the following features are characteristic of the phyletic group Tanaiidae:

Maxillipeds, maxillulae, and mandibulae - unreduced and possessed by all instars including copulatory male.

Ischium article of the pereopods - completely reduced.

Pereopod II - the spinning leg, very slender with a spiniform prolonged dactylus.

Dactylus on pereopods PIII-PVII - well developed as a claw.

Pleonites - reduced from five to four (or three). The first two pleonites with a transverse band of long feathered bristles.

Pleopods - reduced to three well developed pairs.

Pigmentation - dark brownish, blotched and well developed dorsally on the antennulae, carapace, and pereonites.

Behavioural and functional investigations have had low priority in biological studies of crustaceans and other invertebrates. Comparative anatomy has its limitations in the understanding of the living organism, but comparative functional models may be used to distinguish the degree of abiotic impact on the structure as opposed to the biotic, often more complex, processes of evolution.

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REPRODUCTIVE BEHAVIOUR AND LARVAL DEVELOPMENT OF
TANAIS CAVOLINII MILNE-EDWARDS (CRUSTACEA, TANAIDACEA)

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Abstract

Mature female stages are described according to degree of oostegite development. Sexual dimorphism of copulatory males is explained functionally. An aberrant marsupium of two closed ovisacs with a small slit for sperm transfer, is probably for protecting brood from sudden unpredictable changes in salinity. Courtship, copulation, and parental care are described and compared to that of Heterotanaïs oerstedii Kröyer. The different habitats selected by the two species reflect several adaptations in their morphology and behaviour as tube dwellers. A phenomenon unique among invertebrates, that the female T. cavolinii supplies additional yolk to the larvae just before their release, is noted. The production and timing of this food supply is described, and some advantages concerning the larvae's postmarsupial development are discussed.

Introduction

With the exception of Heterotanaïs oerstedii (Bückle-Ramirez, 1965), only a few scattered details are known about the reproductive behaviour of tanaids. The Bückle-Ramirez study describes the behaviour of both sexes with regard to courtship, copulation, brood-care etc.

This investigation of the reproductive behaviour of Tanaïs cavolinii supplements a study on the functional morphology and life history of the species (Johnson and Attramadal, 1982).

T. cavolinii is an almost cosmopolitic inhabitant of exposed tidal hard-bottom habitats and rock-pools. Its body form and behaviour are adapted to tubiculous life. It is about five mm long and spends its entire life confined to the tube and its immediate surroundings. The tube is spun with mucous threads from the spinning legs (PII) and incorporates small fragments from the habitat and the animal's own fecal products.

Earlier works concerning the reproduction of the genus Tanaïs have primarily concentrated on the form (Moers-Messmer, 1936) and number (Iacobescu, 1970) of the ovisacs. Protogynic hermaphroditism has been reported within the genus Tanaïs by Lang (1958).

Material and Methods

A detailed description of the materials and methods has been given by Johnson and Attramadal (1982). The following is a summary:

T. cavolinii builds tubes among the basal parts of the calcareous algae Corallina officinalis and in crevices on the calcified bottom crust. Material for the study was taken from tidal pools on the islets Aspöya and Nord Oddane, near Bergen, on the west coast of Norway. In addition to in situ studies, samples were taken twice a month throughout the year in 1977 for live studies. Morphological and histological analyses were performed on material fixed in 4 % neutralized formaldehyde, alcoholic Bouin and 80 % ethanol. In the laboratory, animals were kept in circulating sea-water of about the same salinity and temperature as their natural habitat (32-34 ‰, 7-15° C). Some animals were allowed to build natural tubes on pieces of C. officinalis, others were offered capillary glass tubes of varying diameters corresponding to different instars. These substitutes were readily accepted. For observation purposes, a Wild M5 dissection microscope movable in all directions above the aquaria, was used. The animals were slowly adapted to light of approximate day-light intensity which was kept constant during the daytime, and which ensured a continual growth of the microflora on the substrate. Under these circumstances, a large number of individuals could be kept alive for months and raise healthy broods.

Results

Development of Ovisacs and the Different Developmental Stages of the Female

The mature female stages are divided according to a terminology used by Gardiner (1975), into the preparatory, copulatory and intermediate stages.

The preparatory stage which involves three moultings, is characterized by oostegites, as yet not developed into a marsupium (ovisac) (Fig. 1 A-C). After the first moult, a single pair of oostegites appear in the form of small lamellae borne on the coxa of PV (Fig. 1 A). After the second moult, the oostegite increases in volume and has the form of a pear-shaped bulb (Fig. 1 B). The following moult increases the bulb to about three times the original volume (Fig. 1 C). The complete preparatory development takes about twenty days at a temperature of 15-18° C.

Preparatory (immature) males were never found and are probably not distinguishable from the female phenotype without histological analysis.

The copulatory stage is characterized by fully developed ovisacs containing eggs or embryones. Copulation takes place after the ecdysis between stages 3 and 4 (Fig. 1 C-D). The eggs are released via the gonopore which opens into the 'stalk' of the ovisac. The ovisacs are an aberrant form of marsupium, each ovisac is developed by only one oostegite. Occasionally, only one ovisac develops

(Iacobescu, 1970). Just prior to copulation, the empty ovisac resembles a shrivelled plastic bag (Fig. 1 D). The eggs are fertilized by the male genital cone probably entering through a small slit in the ovisac membrane. The copulatory female then carries the embryos during their 14-16 day development.

The copulatory male is characterized by distinct sexual dimorphism of the chelipeds, genital cones and pigmentation, and by always being of the same size or larger than the copulatory female.

With the releasing of the young and the loss of the ovisacs, the female enters the intermediate stage. This is identified by the absence of oostegites, and possibly by scars on the coxal plate of PV.

Precopulatory Behaviour of the Male

The only instar that left their tubes, were copulatory males during the breeding season (April to September). This was observed in laboratory and in situ studies. Free walking in search of copulatory females exposed the males to predators such as the isopod *Idotea pelagica* Leach which was observed during daytime catching copulatory males.

When a male came in the proximity of a preparatory female (of stage 3), he approached her directly, tore a hole in the tube wall with the chelipeds, and entered the tube. When the female inhabited a glass capillary tube, he entered through the tube opening.

Precopulatory Behaviour in the Tube

The behaviour in the tube did not seem to follow any strictly fixed pattern, but could be roughly divided into certain phases. At first the female reacted as she would to any intruder by reversing the pleopod beating. If the male touched her antenna (AI, AII), she pressed forwards trying to push him backwards out of the tube, or she used the more defensive method of blocking the tube with her carapax and chelipeds (Fig. 2 A). The male often pumped towards the female with the pleopods. The courtship continued and the turning inside the tube resulted in frequent antenna/antenna and antenna/uropod contact between the two sexes. After some time, the confrontations diminished in frequency and vigour and they seemed to tolerate each other. This usually ended with the male occupying one half of the tube, and the female the other half.

Copulation

Two complete copulations were observed and several copulations were observed in part. The behaviour of the male changed as the female moulted from stage 3 to 4 (Fig. 1 D). The male began approaching the female. To reach her he often had to tear away pieces of exuviae which blocked the tube. At first the female resisted when the male tried to back up to her to place his posterior end ventrally under her, by bending down her carapax or pleon (Fig. 2 A) to block the tube. The male would withdraw and in the pause

both cleaned themselves or ventilated the tube. After several trials, the male succeeded in sliding in under her ventral side, to a position shown in Fig. 2 B. Occasionally, the male was seen to grip the female chela with his own chela, whose aberrant structure seems to fit well around the female chela. In this copulatory position the male genital cones were close to the copulatory slits of the ovisacs for the insemination of the sperm (Fig. 1 D and 2 B). After some minutes, the male distanced himself from the female who immediately started to release eggs into the ovisacs. Within about ten minutes, the ovisacs became voluminous and filled with eggs. During this procedure the female repeatedly kneaded the ovisacs with her pereopods, probably to evenly distribute the eggs and sperm.

A few hours after the copulation, the male left the tube.

Brood Care

During the first postcopulatory period, the female carried out the normal activities described in Johnson and Attramadal (1982). The ovaries never completely displaced the intestine, and the general body-form was kept with only little ventral invagination. The membraneous ovisacs are thin and transparent, with the embryos visible inside. The female continued to knead the ovisacs frequently with the pereopods, which resulted in the embryos shifting position inside the ovisac. The ovisacs did not seem to hinder normal walking or turning inside the tube. Because of their elasticity, they could be squeezed out between the

pereopods or wherever space was available.

After ten to fourteen days, the embryos developed into the larval stage manca II, and the female started spinning a brood-nursery of about three body lengths long (For spatial reasons, the length has been compressed in the drawing Fig. 3). The front section of the tube was partially closed by one or two nets with various openings. Although the rear end was normally closed, the brood-nursery was demarcated to the central part of the tube by an additional posterior net. After this, the female could not vacate the tube and she stopped eating.

To make the transverse nets, she first spun threads on one level, she then proceeded by pulling cemented threads from the outside, through the net, and cementing them on the inside. This closed off the brood-nursery (Fig. 3). Sometimes, an additional net was made on the inside of the first net. The female regularly inspected the net with both pairs of antenna and reinforced it with more threads. Her activity of ventilating the tube resulted in particles getting caught in the nets, which had to be regularly cleaned. The uropods were moved dorso-ventrally, brushing the nets with the bristles, and simultaneously the direction of the pleopod pumping was reversed so that particles brushed off were sucked away.

Behaviour of Larvae in the Ovisacs

Kneading by the pereopods continually shifted the position of the embryos. From 1-3 days before being released from the ovisacs, the larvae developed from the immobile larval

stage manca I into manca II. At this stage they resembled the adults habitually, except that the anlagen of last pereopods and the pleopods were not visible. This manca stage is referred to by Bückle-Ramirez (1965) as the stage with embryogenesis sufficiently completed for the larvae to leave the mothers tube. He describes them as living off "deutoplasma" from the midgut, and thereafter feeding on bacteria, diatoms and detritus from the female's inner tube surface. In the manca II larvae of T. cavolinii the abdomen and most of the thorax were clearly translucent, showing the thin intestine and ventral cord. Two short midgut caeca were developed, sometimes with a small remnant of "deutoplasma". The posterior body was not fully developed, lacking the pleopod and last pereopod anlagen.

When the larvae reached the manca II stage they could walk, and incessantly pinched the ovisac membrane with the chelipeds. On the last day before the release of the young, the female injected through the gonopore a yellow substance, which we refer to as yolk. About one third of the dorsal part of each ovisac was filled up. The mancas immediately started to feed on this yolk, and after some hours most of them had their dilated intestines completely filled up, and they had become yellow. Occasionally, a few mancas did not feed from the yolk and remained transparent. Whether they were delayed in embryogenesis is unknown. If yolk still remained after the release of the larvae, some of them could be seen hanging from it beneath the female, eating.

Release of Larvae

The young were released when the ovisac membrane disintegrated in a matter of seconds, without leaving any fragmental traces. This happened when most of the larvae were filled up with yolk. The two ovisacs disintegrated almost simultaneously. The larvae dropped down and attached themselves to the nearest site on the tube wall. Some were fastened to the wall by the female's spinning. This resulted in a cluster of larvae in the middle of the brood-nursery. The number of larvae varied between 15 and 20. Together with the manca II larvae approximately 3-7 unfertilized eggs or undeveloped embryos, and something which resembled remnants of shed membranes were released.

On one occasion, no yolk was supplied to one of the ovisacs. Only the yolk-filled ovisac disintegrated. The other broke loose at its coxal site after about one day, and was thrown out of the tube by the female, while it still contained living larvae.

Intermediate Female and the Postmarsupial Larvae

The larvae remained immobile in their positions for about five days. Through the glass tubes, the manca II larvae could sometimes be seen scratching and tearing at the inner wall with their chelipeds. Occasionally, larvae loosened from their original places, and started to wander around sluggishly. The female seemed to sense these stray larvae, presumably through contact with her tactile setae, and immediately pushed or dragged them carefully back to the

rest of the group with her chelipeds, attaching them to the wall with spinning threads.

With their first ecdysis, the confined situation of the larvae ended and they moved freely for the first time, as manca III. At this stage, they had become larger and not so transparent. The average length of manca II was 1.0 mm, and manca III about 1.2 mm, but the volume increased approximately 100 %. The pereopod and pleopod anlagen had by now developed. Due to feeding, the intestine became visible as a thin dark stripe. The first food consisted mainly of the diatoms, bacteria and the female faeces on the inner tube surface. After a short feeding period in the mother's pantry, the larvae left by tearing a hole in the tube wall. They made their own tubes using the outside of the mother's tube as substrate. The female soon sealed off the larvae by mending the inside of her tube. She then tore down the transverse nets which had closed off the brood-nursery, started feeding and resumed her normal behaviour.

Discussion

The reproductive behaviour of T. cavolinii shows a strong resemblance to that of H. oerstedii (Bückle-Ramirez 1965).

In both species, the precopulatory behaviour of the male and female is characterized initially by strong confrontations, with the female blocking the tube. This is followed by a period of frequent contact of the antenna, pumping towards each other, and finally by an acceptance of the male's presence.

The behaviour of the copulatory male of T. cavolinii, leaving its tube in search of preparatory females, resembles that of H. oerstedii. The image-forming capability of the eyes of T. cavolinii is poor (Andersson et al, 1978) and certainly does not help locate the female in her well-camouflaged tube. It is possible that localization is assisted by release of a pheromone.

The use of the male chelipeds to grip the female's chela may be one explanation for the sexual dimorphism of this structure. The enlarged opening in the cheliped, caused by the slender shape of the propodus 'finger' and dactylus, fits around the female chela. It may protect the male from being injured if attacked by the female, without damaging her chelipeds. The cheliped may, however, not be essential for successful copulation. According to Bückle-Ramirez (1965), males of H. oerstedii with amputated chelipeds could still copulate successfully. In the case of T. cavolinii this would be most unlikely under natural conditions, as the male cheliped also has other functions. The copulatory male is usually the only free walking instar. When climbing among algae such as Corallina officinalis, the chelipeds are used to grip the rounded branches securely (Johnson and Attramadal, 1982). This is essential for living in an unpredictable and turbulent environment, and may favour the special structural development of the male cheliped.

The precopulatory behaviour of T. cavolinii resembles that of H. oerstedii, except for details of copulation which are probably a consequence of the morphological differences between the species. While the female

H. oerstedii opens her marsupium wide to receive the sperm of the male, the two ovisacs of T. cavolinii only have small genital slits medio-ventrally positioned to meet the male's genital cones. Through close contact with the female's ovisacs and through his movements, the antero-ventrally directed genital cones probably open the slits and point directly into the ovisacs. To ensure fertilization of both ovisacs, it is essential that the genital cones are of the dikonophoran type. After the copulation, the female H. oerstedii moves her oostegite lamellae, probably to mix sperm and eggs, while the female T. cavolinii kneads the ovisacs to obtain the same result.

The eggs are laid into the ovisac via the gonopores which are the ovisacs' only connection with the body. In H. oerstedii, the egg-filled ovaries occupy the thorax almost completely, displacing other organs such as the intestine. After the eggs are released into the marsupium, the ventral side of the female invaginates, leaving additional room for embryos without considerably enlarging the total diameter of the marsupium and the body. This is important for a tube-dweller. In T. cavolinii, the ovaries never completely displace the intestine and the normal body-form is kept by the female, with little ventral invagination. This allows the female to feed until she confines herself to the brood-nursery during the last days of the copulatory stage.

The function of the frequent kneading of the ovisacs is uncertain. Several other peracaridan crustaceans ventilate their brood more or less regularly by a pumping action of the marsupial lamellae, e.g. mysids

(Tattersall and Tattersall, 1951), the isopods Idotea neglecta G.O. Sars (Kjennerud, 1951) and Astacilla sp. (Schiecke 1973), the tanaid H. oerstedii (Bückle-Ramirez, 1965) and species of Apseudes (Schiecke, 1973). For T. cavolinii, this type of ventilation is impossible. The thin ovisac membrane probably permits some diffusion of oxygen into the ovisac. The kneading may fill the same purpose as ventilation, by shifting the position of embryos, circulating the ovisac-fluid, and preventing embryos from lying continuously in areas deficient in oxygen.

Other crustaceans inhabiting osmotically variable environments, such as the mysid Praunus flexuosus (Müller) are known to osmoregulate the contents of the marsupium (Mcclusky and Heard, 1971). The ovisacs of T. cavolinii are completely closed off. This may be necessary for protection of the embryos against the sudden extreme variations in salinity which frequently occur in tidal pools. We have not, however, tested the ability of T. cavolinii to osmoregulate the ovisac contents.

The brood-nursery behaviour resembles that of H. oerstedii, in that the larvae are kept in a restricted part of the tube, and the female retrieves stray larvae. The two species differ, however, in the timing of the construction of the brood-nursery. H. oerstedii seals the tube opening immediately after the male has left the tube, and it remains sealed until the larvae have left the tube. The female cannot feed during this period. The female T. cavolinii can feed during the copulatory stage until she constructs the brood-nursery some days

prior to the release of young. This additional feeding may be necessary for the large amount of yolk which is produced during this period.

According to Bückle-Ramirez (1965), the loss of embryos from the relatively open marsupium of H. oerstedii is a common event, and it is therefore necessary for H. oerstedii to seal off the tube directly after the copulation. The closed ovisacs of T. cavolinii completely eliminate this. The functions of the brood-nursery suggested by Bückle-Ramirez (1965) are: (1) 'Eggs' and larvae are protected from being washed out of the tube. (2) By the pleopod pumping of the female, diatoms are sucked into the tube, fasten onto the inner tube wall, and serve as food for the newly released larvae. (3) The brood-nursery serves as protection. The brood-nursery of T. cavolinii functions in much the same way. The female is very intent on keeping the larvae in a group, and transverse nets may serve as barricades, temporarily preventing stray larvae from leaving the tube until the female can locate and retrieve them.

Regular cleaning of the transverse nets of the brood-nursery prevents clogging, and may save energy by making the pleopod pumping more efficient. The cleaning procedure reveals an additional function of the uropods, besides that of being tactile sensory organs.

The yolk undoubtedly functions as additional nourishment for the larvae. In this case this is accomplished by transforming the succeeding generation of eggs in the ovaries into food for the larvae. This 'lactating' or second

investment of yolk in the progeny makes T. cavolinii unique, at least among crustaceans. A number of advantages may be put forward: the yolk may increase the growth rate and the size of the larvae, the female saves energy by not investing yolk in the eggs which do not develop into manca II larvae, and she has extra time to accumulate energy for the development of eggs and yolk.

The disappearance of the ovisac membrane does not seem to come about by mechanical means, because it happens abruptly and tracelessly, without any noticeable activity from the larvae or female. An enzymatic dissolving of the ovisac membrane is more probable. A similar dissolving of the oviductal sac is known among cirripeds (Barnes and Blackstock, 1977). The question is whether the female or the larvae produces the enzyme to set off the dissolving of the membrane, which does not occur until most of the larvae have their intestines filled with yolk. When the larvae did not receive any yolk, the ovisac membrane also did not dissolve. This points towards the larvae as releasers of the enzyme. The absence of yolk was, however, probably caused by a pathological disturbance which similarly may have prevented the female from releasing the enzyme.

Some undeveloped eggs or dead embryones, and remains of shed membranes, were generally released with the manca II larvae. This is not reported for H. oerstedii.

Bückle-Ramirez (1965) remarks that the female cleans out the marsupium with the pereopods. She also has a mechanism for returning lost embryos, except for those which deviate from normal size, which are eaten. The closed ovisacs of T. cavolinii prevent the cleaning out of unfertilized eggs, dead embryos and membrane remains, which are therefore released with the young.

Altogether, there is a considerable likeness in the reproductive behaviour of H. oerstedii and T. cavolinii, although the environmental conditions in the habitats of the two species may differ considerably. H. oerstedii lives beneath the surface of soft mud, and T. cavolinii on the substrate of exposed rock-pools. This difference is reflected in several details of morphology and behaviour. Likewise the common features must have been acquired as a result of a tubiculous life strategy in a variable, shallow marine environment.

It is too early to determine whether this pattern applies to other tanaids. As H. oerstedii and T. cavolinii are the only investigated species to date, more varied studies on biology, functional morphology and behaviour are needed to establish the existence of a general tanaid-pattern.

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Legends

Fig. 1. The development of the oostegite into an ovisac.

All views are lateral, except for D, which is a medial view.

A-D. Preparatory female stages 1-4. Increase in size of oostegite by subsequent moultings.

D. Developed ovisac with genital slit through which sperm is transferred. No further moults occur during the marsupial development (D-G).

E. Ovisac filled with eggs or early embryos.

F. Embryones before hatching to manca I larvae.

G. Manca II larvae feeding on yolk.

Fig. 2. Courtship and copulation.

A. Copulatory male entering female tube. Typical female pose when blocking the tube with the carapax.

B. Position during transfer of sperm with the male genital cones entering the female genital slits.

Fig. 3. Female and post-marsupial larvae in brood-nursery, showing transverse nets, a group of released larvae fastened to the tube wall digesting the yolk, and newly moulted manca III larvae leaving the brood-nursery, and making their own tubes.

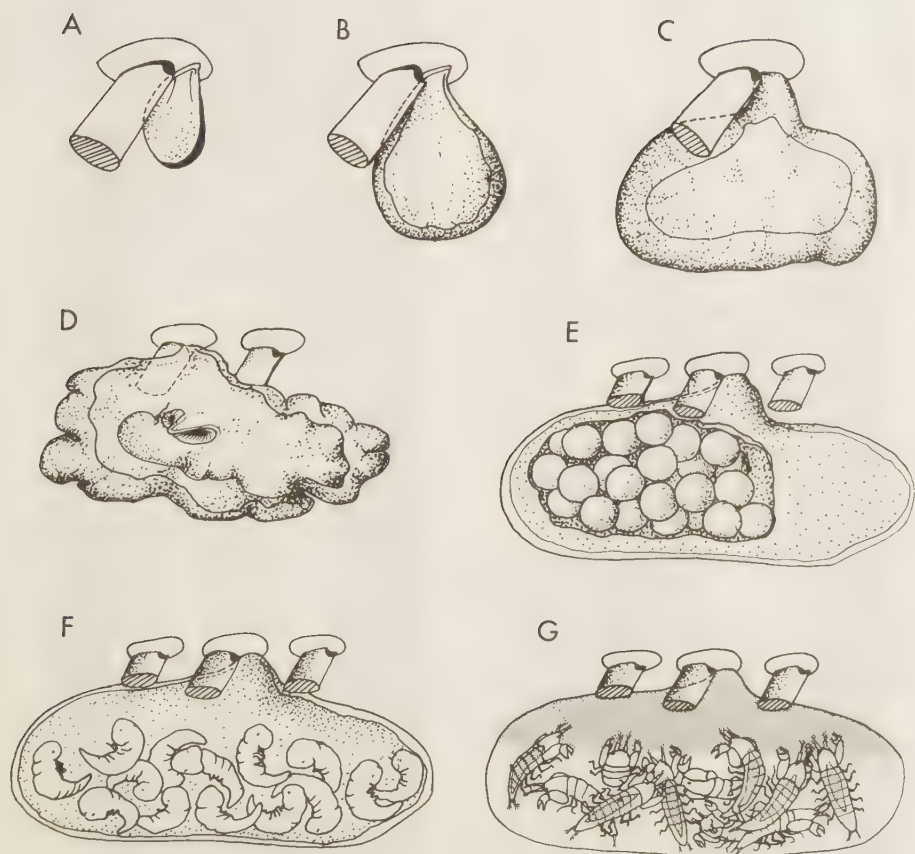


FIG. 1

A



B

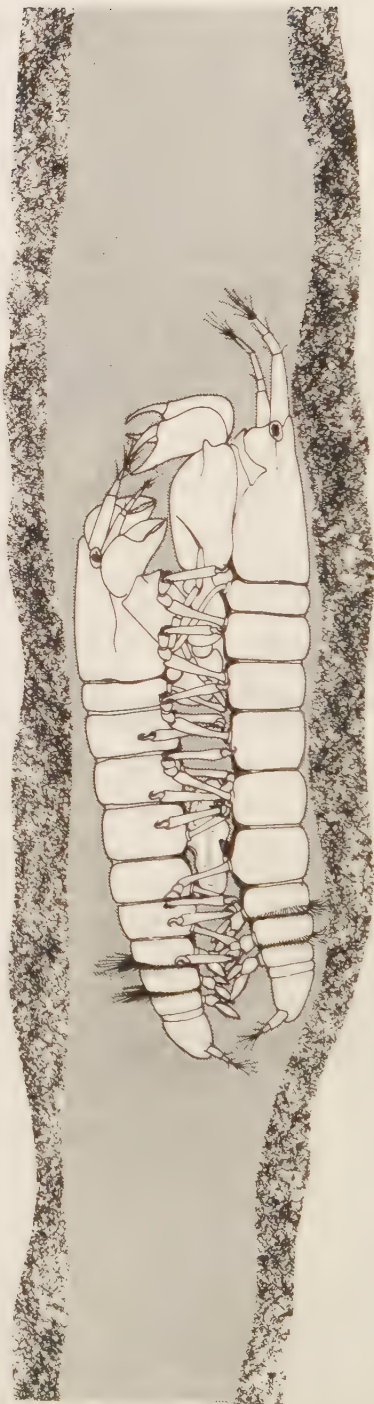


FIG. 2

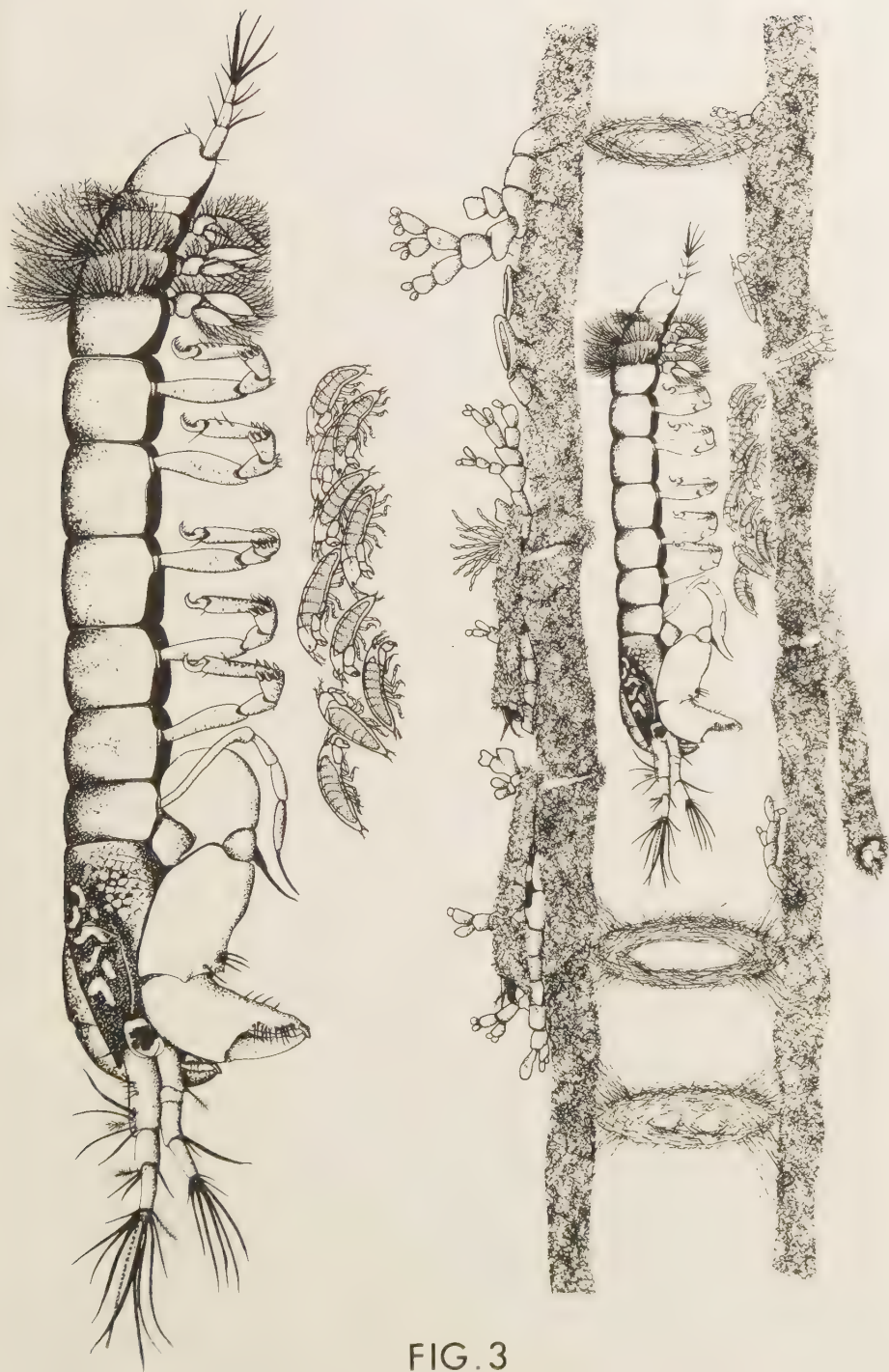


FIG. 3

THE REPRODUCTIVE STRATEGY AND DISPERSAL OF
TANAIS CAVOLINII MILNE-EDWARDS (CRUSTACEA, TANAIIDACEA)

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ABSTRACT

The study is based on live-observations, functional analyses of structures and in situ studies. Facing uncertain environmental conditions at the time of reproduction, the female minimizes reproductive costs by producing small eggs with a minimal amount of yolk. If the brood survives a 'critical stage', the eggs simultaneously developing in the ovaries are transformed into yolk and sacrificed as food for the developing young. If not, the female can fall back on the new generation of eggs. The impending risk of a complete or partial brood loss is counteracted by the female making the final energy investment when the young have passed the 'critical stage' in their embryonal development. The yolk-feeding results in larger larvae which means increased survival capacity. This two-phase nourishment strategy likens Mammalia in that nourishment is supplied once for embryonal development, and again at a later stage to aid the development of viable young. This strategy complies with the 'bet-hedging' hypothesis by Mountford (1973). In the unpredictable environment, where local populations (each rock-pool represents a local population) continuously risk extinction, survival of the total population is favoured by a strategy of protogynic hermaphroditism, which results in individuals with alternating sexes. This means that all propagules of a new population may participate as females in the production of offspring, and thus increase productivity rate and recolonization capability. Each isolated local pool can be regarded as a 'gene-bank' for the dispersed population, with genetic communication occurring frequently. Such a well-adapted survival strategy in local habitats may also explain the world-wide distribution by passive drifting on tufts of algae, as no pelagic larvae exist.

INTRODUCTION

The tube-dwelling tanaid Tanais cavolinii (Milne-Edwards) is an almost cosmopolitic peracaridan crustacean inhabiting rocky tidal environments and rock-pools. Supratidal rock-pools are most exposed to drastic changes in turbulence, temperature, salinity, insolation and oxygen content. Unpredictable events like drainage and the impact of ice could result in extinction of local populations. Under favourable environmental conditions, however, this habitat may be ideal for breeding and development, offering calm and sheltered water with higher temperatures and an increased availability of food. The habitat is characterized by dense carpets of algae (e.g. the calcareous alga, Corallina officinalis) which act both as a substrate for food (epiphytes and diatoms) and as protection. This tanaid, about five mm in length, lives its entire life confined to a tube and its immediate surroundings. No pelagic stages exist and their ability to swim or walk is very limited. Adaptations to the environment, developed by T. cavolinii, have recently been described by Johnson & Attramadal (1982a). This includes specific reproductive behaviour to ensure survival of the larvae. However, reproduction poses problems such as how local populations in tidal pools exist despite desiccation and ice, and how recolonization of such sites comes about. World-wide distribution of the species also seems curious considering the lack of pelagic larval stages. These more general aspects of reproduction and dispersal are dealt with in this paper.

MATERIAL AND METHODS

Material was obtained from tidal pools on the islets Aspöya and Nord Oddane, near Bergen, on the west coast of Norway. In addition to in situ studies, samples were taken twice a month throughout the year in 1977, for live studies and for investigation of the population structure. Morphological and histological analyses were performed on material fixed in 4% neutralized formaldehyde, alcoholic Bouin and 80% ethanol. In the laboratory, animals were kept in circulating sea-water of about the same salinity and temperature as their natural habitat (32-34‰, 7-15° C). For further details concerning methods for live studies, see Johnson & Attramadal (1982a).

For an interspecific comparison of egg-size in correlation to female body size and number of eggs produced in different tanaid species, see Table 1.

RESULTS

Egg number and egg volume of *T. cavolinii* as compared to other tanaid species

Intraspecific variation in the number of eggs produced may depend on the size of the female, age of maturity, available food etc., but it is difficult to establish egg numbers accurately due to inadequate sampling techniques.

The number of eggs presented (in Table 1) for each species thus represents the highest number of eggs found in the marsupium.

T. cavolinii deviates from other tanaids by its capability of producing a much larger number of eggs per brood, with a maximal number of 46 compared to 29 for the large A. spinosus and 6 for the smallest Pseudotanaïs forcipatus (Lilljeborg).

Egg diameters are measured (intraspecific variation of approximately 10%) for six tanaid species of differing size, the smallest species being 1.4 mm and the largest 13 mm. There is a positive correlation between total egg volume and species female body length, significant at the 0.001 level (Table 1).

T. cavolinii deviates with comparatively smaller eggs ($4.5 \mu^3 \times 10^6$) but which is compensated for by increased number (46). Except for the smallest species (1.4 and 2.0 mm), all other species produce larger eggs. Egg volumes for other peracaridan crustaceans of a similar body size can be used as a comparison e.g. for the smallest pelagic mysid (2.5 mm), the egg volume was $16.9 \mu^3 \times 10^6$ (Mauchline, 1973), and for the smallest benthic cumacean, egg volume was about $15 \mu^3 \times 10^6$ (Corey, 1981).

It is possible that some tanaid species, being the smallest among peracaridan crustaceans have small eggs which have to be spaced out like a string of pearls for spatial reasons. T. cavolinii, however, has space enough in the body to produce larger eggs. In the small species Heterotanaïs oerstedii (1.5-2.2 mm) which has a slender body, even the smallest eggs of 170 μ can be spaced only with help of sternal evagination

TABLE 1

SPECIES	(X) female body length (mm)	($\bar{X}$) (mm)	(Y) Egg-volume ($\mu^3 \times 10^6$)	(n) number of eggs	Total egg- volume (Yxn) ($\mu^3 \times 10^6$)	No. ovigerous females	Tot. no. specimens
1. <i>Pseudotanaïs forcipatus</i> Lilljeborg	1.3-1.5	1.4	2.8	4	11.2	5	16
2. <i>Heterotanaïs oerstedti</i> Krøyer	1.8-2.3	2.0	2.8	16	44.8	-	-
3. <i>Typhlotanaïs tenuimanus</i> Lilljeborg	3.9-4.5	4.2	6.3	18	113.4	8	35
4. <i>Sphyrapus serratus</i> G. O. Sars	4.5-5.3	5.0	17.2	20	344	3	61
5. <i>Tanaïs cavolinii</i> Milne-Edwards	4.3-5.7	5.1	4.5	46	207	20	∞
6. <i>Apseudes spinosus</i> M. Sars	10.6-12.9	12.0	33.5	29	972	7	50

The relationship of female body length, egg-volume and total egg-volume of six tanaid species. Figures given for the number of eggs (n) represent maximum number of eggs found in the marsupium.

There is a positive correlation between total egg-volume and species female body length. (Spearman's $\rho = 0.98$, significant at the 0.001 level)

Locality and Remarks

1. Öresund, Sweden (Sept. 1977)
2. Data from Bückle-Ramirez (1965), Scholl (1963)
3. Herdla fjorden, Norway (July 1977)
4. The Norwegian Sea ('NORBI' sta. 2, 3, July 1975)
5. West Bergen, Norway (Aug. 1976)
6. Gullmarsfjorden, Sweden (Dec. 1981)

of the body. Accordingly, a sternal invagination is needed for spacing the eggs in the marsupium. As a result, the inner organs are cramped and the depressed intestine prevents feeding. In T. cavolinii this does not occur as the small eggs are well spaced in a comparatively much larger body.

Egg and larval development

After copulation, the female releases the eggs into the ovisacs and starts producing new eggs in her ovaries which develop parallel with the embryos in the ovisacs. Although the closed-off ovisacs presumably function as protection against extreme environmental conditions, high mortality of embryos may occur during a 'critical stage' in the embryonal development. The number of eggs in the ovisacs varied between 20 and 46 while the released larvae numbered 15-20. If the brood fails, the female has a new generation of eggs already developing in her ovaries and may breed again without delay. If the brood survives to the second larval stage (manca II) (Fig. 1), the subsequent generation of developed eggs are transformed into yolk and supplied to the progeny as food, before their release from the ovisacs. The continued postmarsupial development period during which the yolk is digested, results, after first moult, in well developed larvae (manca III) which are capable of feeding and spinning their own tubes.

This unique form of larval development may be a specific adaptation for T. cavolinii. Usually, yolk is invested only in the egg, so that larger eggs may produce larger larvae with an increased probability of survival (Christiansen & Fenchel, 1979).

Postmarsupial development

The destiny of the independent young in their natural environment has not been investigated. In the cultured population the young developed from juveniles, through three stages as preparatory females (Fig. 1). Unfortunately, no individuals matured enough to breed. No males developed from the juveniles in the cultured population. This seems to verify the theory of potential protogynic hermaphroditism, which states that juveniles may first develop into females and change into males when necessary, or favourable, or that the juveniles may develop into males or "neutra" (Bückle-Ramirez, 1965). When Bückle-Ramirez experimented with isolated larvae, they only developed directly into so called "primärmänchen" (i.e. males lacking secondary sexual characters) in the presence of mature females, and in the absence of other copulatory males. The phenomenon of hermaphroditism in Tanaidacea was also reported by Forsman (1956), Wolff (1956), Lang (1958) and Gardiner (1975).

LARVAL AND POSTMARSUPIAL DEVELOPMENT

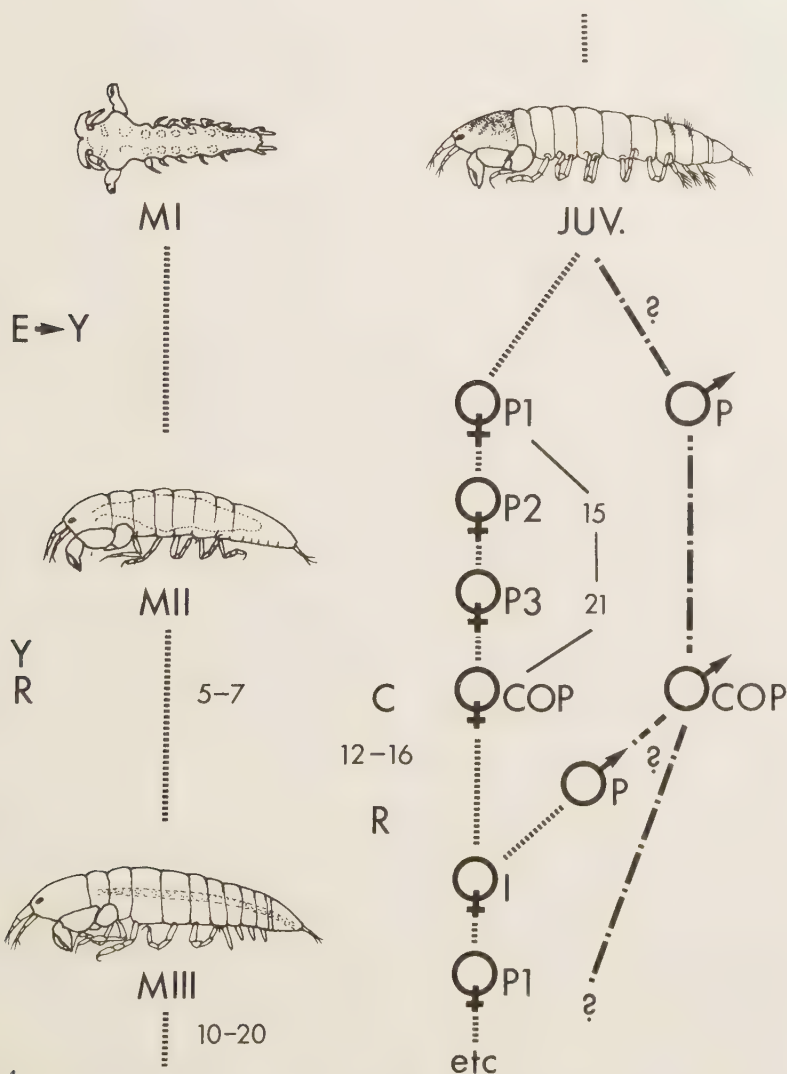


Fig. 1.

The development of manca larvae (MI-III) from the 'critical stage' (MI) after which the new generation of eggs is transformed into yolk (E→Y). When moulted into manca II the yolk is supplied to the larvae (Y), which thereafter are released from the marsupium (R). The manca III, PVII and pleopod-anlagen visible, feeds and makes its own tube. After moulting into juvenile stage, the development is suggested to be protogynic hermaphroditism. After three preparatory stages (P1-P3) the female copulates (C) and enters the copulatory stage (COP). The subsequent intermediate stage (I) can be followed by repeated breeding or development into preparatory male (P). Figures represent time in days and ? indicates uncertain paths.

Post-breeding development of the female (Fig. 1)

After the larvae vacate the tube, the female leaves the copulatory stage and moults into an intermediate stage (oostegite anlagen not visible). It is uncertain what determines the following stage of her development, but she may moult into a preparatory stage and start developing eggs again (a female may under favourable conditions produce several broods during a breeding season), or she may develop into a copulatory male. That females of T. cavolinii, after raising broods, can develop into males is supported by the results of the following experiment: Intermediate females were isolated from the cultured population and placed in Petri-dishes so that water-contact with other instars was broken. After some weeks they moulted into the 'preparatory male' stage with developed genital cones distinct pigmented, but lacking the characteristic well-developed copulatory male chelipeds.

Population structure and sex ratio of the natural population

Copulatory males can be distinguished from other instars by the sexual dimorphism of the chelipeds and well-developed, darkly pigmented genital cones. Mature females can be distinguished from juveniles or "neutra" by the oostegites (preparatory females) or ovisacs (copulatory females) or by scars left by the ovisacs (intermediate females) (Johnson & Attramadal, 1982b).

For the population investigated on the west coast of Norway, the breeding season started in April and ended in September. The winter population (in March) consisted of appr. 90% female phenotypes (immature females or neutra) and appr. 10% large copulatory males.

During the summer-season, the population structure was: approximately 10% copulatory males, 10% copulatory females, 50% preparatory females, 20% neutra, and 10% small juveniles or manca larvae (number of manca and juveniles uncertain). In March, the largest instars were copulatory males which had over-wintered. In more well-established and denser populations ($10\ 000/m^2$), small instars of the copulatory male phenotype were never found. The instars which over-winter and develop into copulatory males, probably die after the early reproductive period (April - June), and are continuously replaced by instars which over-wintered as neutra or by intermediate females developing into copulatory males.

According to Bückle-Ramirez (1965), females of H. oerstedii favoured males of equal or larger sizes. The smaller males' inability to compete with larger males may explain the absence of small copulatory males in dense populations of T. cavolinii. That males are only distinguishable among the largest instars, supports the theory of potential protogynic hermaphroditism.

DISCUSSION

I will attempt to analyse the peculiar reproductive strategy of T. cavolinii, bearing in mind the problems of survival, recolonization and dispersal.

Larger eggs and larvae generally have an increased capacity for survival (Christiansen & Fenchel, 1979). The disadvantage of undersized eggs which usually means decreased viability of the young is counteracted by the female's strategy of feeding the larvae with the new generation of eggs. The female benefits by making the final energy investment only when her young have passed the 'critical stage' with a fair chance of survival. This is favourable considering the impending risk of complete or partial loss of the brood. In this eventuality, the female has already started a new generation of eggs and may soon copulate again. If the brood survives, the female has had extra time to produce the additional expenditure of yolk that is needed for continued development of the larvae.

If the amount of yolk, which is given to the young in the postmarsupial stage (about twice the original egg volume) were to be present in the egg, the volume of the egg would be tripled. This would give rise to spatial problems and a decrease in the number of eggs. As smaller investments are made in each egg, the yolk wasted on unfertilized eggs and dead embryos in the ovisacs is minimal.

If less space is required, the females can produce eggs at an earlier age (smaller body size). Alternatively, under

unfavourable conditions, she can delay maturation, and with an increased body size can invest in a larger number of eggs, maximizing the brood size. As the female cannot predict when conditions will be favourable enough for the male to visit (Johnson & Attramdal, 1982b), she alleviates the risk of being unprepared for copulation if she matures early. Another advantage of smaller eggs is that she may feed unhampered, even while carrying eggs.

Smaller eggs could benefit from a shorter development period, as this minimizes the risk of bad conditions coinciding with the 'critical phase' of embryonal development in the ovisacs. The difference between the number of eggs and the number of larvae which develop, and the presence of dead embryos point to the existence of a critical stage during the 12-16 day embryonal development. As the duration and time of favourable breeding conditions cannot be predicted, it is favourable that many broods be raised during each period and that the female be capable of breeding in short time after possible brood failure. That means more chances to successful broods.

Adults and released larvae are adapted to strong and sudden variations in salinity, temperature and oxygen. Adults can survive anoxic conditions for shorter periods (Gamble, 1970). The embryos are protected by the closed-off ovisacs which the female may osmoregulate, but it has not been ascertained how the embryos are supplied with oxygen.

The large, relatively few males may be a consequence of protogynic hermaphrodite potential. In well-established populations of T. cavolinii, of which 10% are large copulatory males, it is more favourable that young instars first develop into females and later into males, when they have become the largest instars, have raised one or more broods and are competitive enough to function as copulatory males. The 10% average of copulatory males present during the reproductive season, were previously the overwintering neutra, or more probable, intermediate females which had raised one or more broods. In this way, one may ensure a constant average proportion of 10% copulatory males to 10% copulatory females among adult instars during the breeding season. Potential protogynic hermaphroditism thus results in individuals with alternating sexes.

If among propagules, there were one with protogynic hermaphrodite properties, it could spread its genes to the new population, and in this way establish this strategy. This phenomenon would become a stable strategy for survival in an unpredictable environment.

Exposure to waves during storms breaks loose tufts of C. officinalis and other material together with T. cavolinii tubes, some of which are washed out to sea and others washed up on cliffs, in crevices, and in small rock-pools. In this way, the population spreads to many isolated sites which may be favourable or as unpredictable as the previous ones, but the risk of total extinction is minimized. High colonization capability and high productivity rates are favourable.

All the propagules in the new population, except copulatory males, may participate in the production of eggs with this strategy.

This strategy of reproduction and dispersal has probably been evolved to ensure survival in a system of rock-pools. The isolated rock-pools can be regarded as 'gene-banks' for the dispersed population, with genetic communication occurring frequently. Such a strategy is not likely to have evolved for long distance dispersal a priori, because the chances of a propagule surviving on drifting algae are very small, and calcareous algae do not float. Nevertheless, T. cavolinii has world-wide distribution in marine tidal zones, lacking dispersal stages (planktonic larvae) and with a poor ability to swim or walk. If distribution were to be explained by passive drifting on tufts of algae, a prerequisite for successful colonization would be efficient strategies for reproduction and dispersal, well-adapted for survival in local habitats.

The impending risk of a complete or partial brood loss is counteracted by the female making the final energy investment only when the young have the best chances of survival. The yolk-feeding results in larger larvae with an increased survival capacity which increases the probability of offspring. This strategy complies with Mountford's 'bet-hedging' hypothesis (Mountford, 1973). At the individual as well as the population level, 'bet-hedging' stresses the importance of not only maximizing the number of off-spring produced, but also of minimizing the probability of leaving no young at all.

Potential protogynic hermaphroditism may thus result in a better recolonization ability, an increased reproductive capacity within each local population, as well as increased chances of spreading the genes to several local sites. In this way, the population has a decreased risk of extinction.

T. cavolinii and its few relatives represent an 'evolutionary dead end' among dikonophoran tanaids. By adapting to exposed tidal habitats, it has become a phyletic line, incapable of inhabiting more or less soft substrates, like other dikonophoran groups.

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A FUNCTIONAL-MORPHOLOGICAL STUDY OF THE TUBE-DWELLING
APSEUDES SPINOSUS M. SARS (CRUSTACEA: TANAIIDACEA),
AND A COMPARISON WITH DEEP-SEA TANAIIDACEA

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The study is based upon a functional analysis of the structural plan of Apseudes spinosus with regard to ecological adaptations, and a comparison of these data with homologous structures in the deep-sea taxa, Sphyrapus and Neotanais. The functional model of A. spinosus corresponds to that of the tube-dwelling tanaid, Tanais cavolinii with regard to joints and articles of the pereopods, and the location of spines and setae. Tunneling involves the antennulae, chelipeds, IInd pereopods and all the other legs, and would not have been possible with only the 'fossorial limbs' (PII). Their stout bordering spines facilitate tunneling in mud intermingled with stones and gravel, and can therefore be regarded as an adaptation to this kind of sediment. In Neotanais, the IInd pereopods are not so fossorially accentuated yet they probably function analogously in homogeneous, soft sediment. The small rudimentary exopodites characteristic of monokonophoran tanaids and present in A. spinosus have a protective function and assist in respiration. In the dikonophoran, Neotanais, the elongated furrows on the carapace which are respiratory pores are protected from fouling exteriorly by a close lattice-work, and interiorly by the terminal brush of fine setae on the epipodite. Pleopods are well-developed in both groups, and are used for ventilation and for assisting respiration by producing a water-current through the tube. Both A. spinosus and Neotanais have homologous structures that seal off various parts of the pleon, preventing lateral and dorsal recirculation and thus increasing pumping efficiency. The large amount of common characters within the two phylogenetic lines, Neotanaidae and Apseudidae, must have arisen through convergent and/or parallel development, as adaptations to similar abiotic environmental conditions, for tunneling and for tube-dwelling. Certain morphological differentiations are the result of differing kinds of substrates, which may also explain the diverging geographical distribution of these taxa. Evaluation of taxonomic characters should therefore be considered in the light of these factors.

1. INTRODUCTION

For an improved understanding of the deep-sea tanaids, their life-history and evolution within their habitat, there is a need for basic data concerning functional morphology and ecology. This may be accomplished by means of in vivo observations and experimental studies on live specimens as is done for studying shallow water forms (BÜCKLE-RAMIREZ, 1965; JOHNSON and ATTRAMADAL, 1982a). However, deep-sea cruises are rare events and moreover many deep-sea organisms may be stenotopically adapted to salinity, temperature and light, which poses serious problems when using traditional collecting gears for deep-sea research. Modern protective cod-ends for the recovery of live deep-living animals have recently been designed and used satisfactorily on midwater organisms (CHILDRESS et al., 1978) and on benthic organisms (JOHNSON and ATTRAMADAL, 1982b), so that prospects for future deep-sea studies have improved. In the meantime, as an alternative one may study close relatives of exclusive deep-sea species, or species with a wide vertical distribution which often live more shallow in boreal or arctic waters. Apseudes spinosus (M. Sars) belongs to the second category and is distributed along the west-coast of Sweden and Norway at depths varying from 300 to 1400 m. It has a close relative in Sphyrapus serratus (G. O. Sars) which has a vertical distribution down to 3200 m in the Norwegian Sea. In the Swedish Gullmarsfjorden, there is a shallow locality of 50 m which is a refuge for the A. spinosus, used as live material for this study.

Thus, this study: 1) analyses the structure of Apseudes spinosus with regard to its function in order to improve an understanding of its ecological adaptations, 2) compares these data to homologous structures of the deep-sea taxa of Sphyrapus and Neotanaisidae.

2. MATERIALS AND METHODS

A. spinosus, from Gullmarsfjorden, was obtained during winter because with lower surface temperatures there was less risk of harming the animals. Apseudes were adapted to small, flat aquaria (5x20x40 cm) with habitat sediment, low intensity light and circulating sea-water with a salinity of 35‰. The sediment consisted of loose mud clay with gravel, stones and bivalve shell-fragments intermingled. Tubes or tunnels were often made under pieces of shells. By replacing the shells with thin glass plates left on the sediment surface, animals could be observed dwelling in and making their tubes. Observations were made through a dissection microscope in weak yellow light, and with the use of Infra-red (IR) equipment (SAVEN Find-R-scope, FJW Industries). Some fifty animals were kept alive for over a year and even raised healthy broods.

Sphyrapus serratus was obtained from deep-sea localities in the Norwegian Sea (sta. 4. 69°O, 14'N; 04°O, 18'E, 3213 m) and Neotanais spp. from the North Atlantic (sta. 8. 55°O, 02'N;

12°O, 34'W, 2890 m) during the NORBI and INCAL expeditions of 1975 and 1976, respectively. No live specimens were retrieved. The material was preserved in neutralized formaldehyde (4 %) and alcoholic Bouin. Some of the material was prepared for SEM according to NIELSEN and STRÖMBERG (1973), and investigated by means of a Mark II Cambridge Stereoscan.

The other species and species-groups of Neotanaidae, which are morphologically compared in the discussion, are described by GARDINER (1975).

3. RESULTS

Walking and tunneling

Walking was occasionally noted when specimens were placed on unfavourable substrates (stone) or on a thin layer of sediment. Only the pereopods III-VII were used for walking. The articles of the pereopods are hinged to each other and to the body at such angles that the optimal working position of the legs is in a V-form (Fig. 1). Thus, the extension of the leg is restricted and unsuitable for walking on a flat surface. The procedure is slow and inefficient as a means of locomotion.

An ability to swim was never demonstrated, although several tests were made on specimens released free in a water column.

Tunneling is a complicated procedure. The first appendages to penetrate the sediment are the antennulae, which are extended straight forward and enclosed and protected laterally

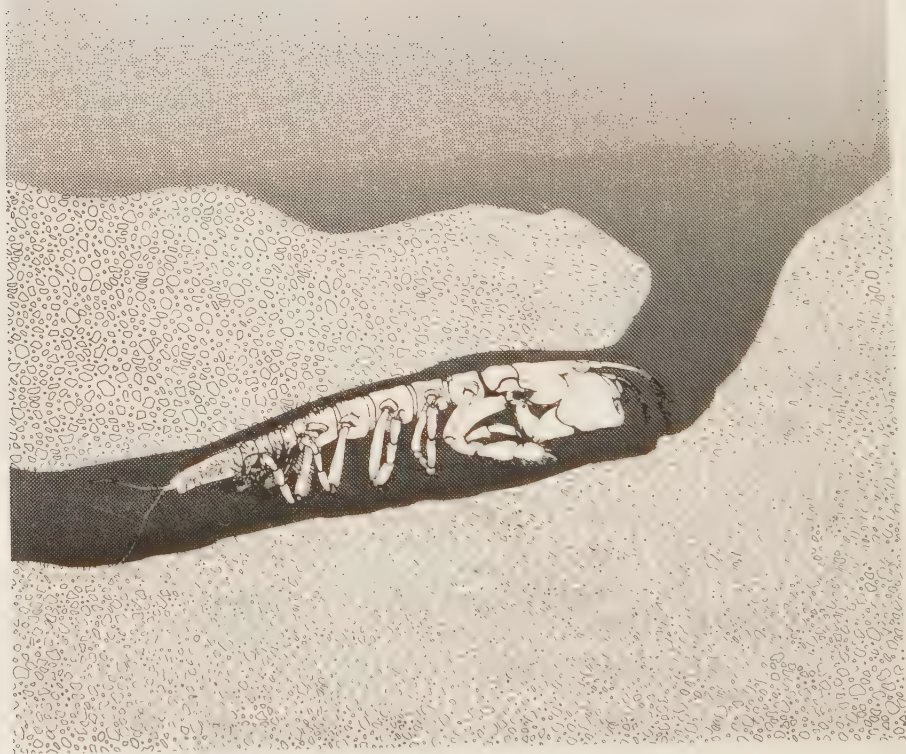


Fig. 1.

Apsseudes spinosus in its tube (longitudinal section), close to one of the two openings, recognizable on the surface as small funnels. The optimal inverted position (V-form) of the legs PIII-PVII is seen. The long pleon, embedded in mud, functions as a smooth seal.

by the fossorial pereopods. Thereafter the chelipeds, act like a plough. The strongly developed spines borne on the propodus of PII (Fig. 2A) act in a saw and pitch-fork combination behind the plough, forcing coarse material to the sides and making way for the legs (pereopods III-VII). With the use of these legs, the tunnel is enlarged and the sediment packed together to strengthen the tunnel wall. These legs are not fossorial, but rather more slender and adapted for locomotion. Their working positions are orientated for PIII-PIV anteriorly, for PV straight laterally and PVI-PVII posteriorly.

Tube building (tunneling) and the locomotionary adaptations involved

No cementing glands and spinning threads are used for reinforcement of the tube as is the case for other tanaids (BUCKLE-RAMIREZ, 1965; GREVE, 1967; JOHNSON and ATTRAMADAL, 1982a), so the tube is prevented from caving in by means such as the trampling of a dust floor, and the packing of fine sediment into the walls with the aid of the pereopods. Coarse sediment is handled by the fossorial PII. Finer sediment is packed by the other legs which have special arrangements of setae on the distal part of the carpus and propodus, which act on the surface like the disc of a ski-pole, with the spiniform dactylus acting as pole and the propodal and carpal setae as the disc (Fig. 3, Pl. I, A-C). By repeated trampling with the help of these devices, the sediment is packed to give a stable inner structure to the tube.

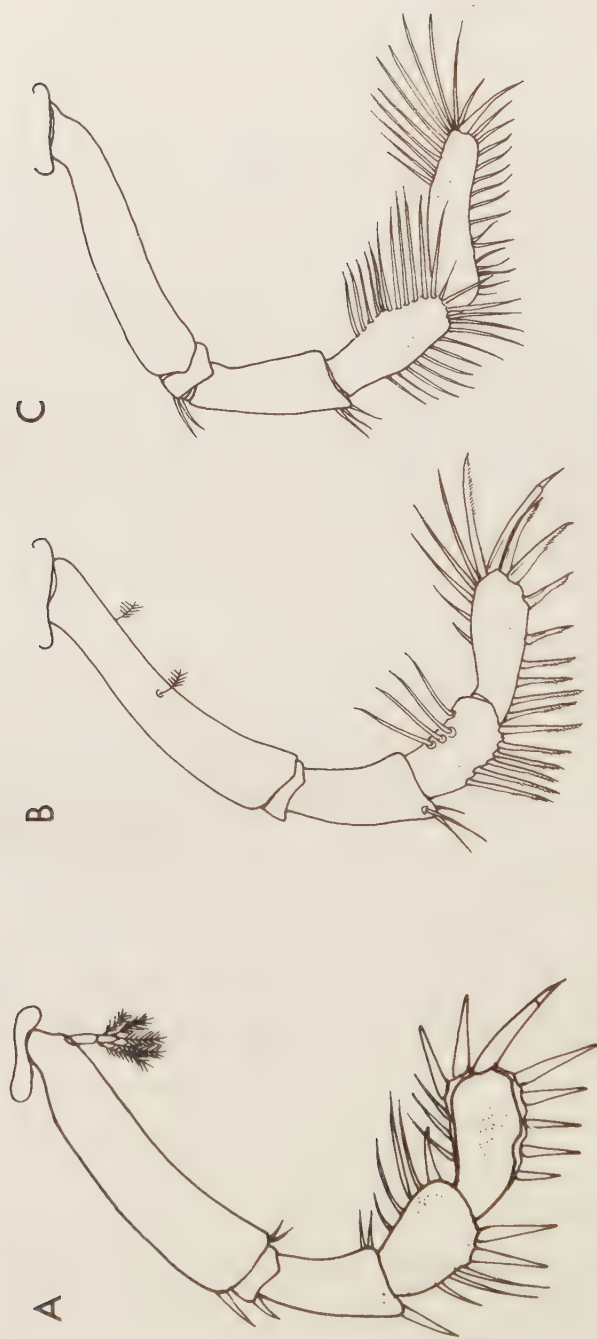


Fig. 2.

- A. *Aapseudes spinosus*, IInd pereopod with strongly developed spines.
 B. *Neotanais americanus*, IInd pereopod with stout spines mixed with slender bristles.
 C. *Neotanais robustus*, IInd pereopod, richly furnished with slender bristles.

The fragile tube makes lithe movements and slender appendages necessities. The heavy chelipeds and fossorial legs are kept close to the sides of the carapace. For locomotion back and forth the 'ski-pole arrangement' is used. The delicate flagellae of antennulae and antennae are kept in tactile contact with the surrounding. The very slender multi-articulated uropods act in the same manner. With these structural adaptations, A. spinosus can move rather quickly inside its tube.

The setation and cuticular configurations of carpal and propodal articles of pereopods developed for tube-building and locomotion described for apseudids correlate with those of neotanaids (Pl. I, D) (See also GARDINER, 1975). These articles on the 'fossorial' legs (PII) are not as fossorially expressed in Neotanaeis, but are richly furnished with long bristles and also with long, less stout spines, covering about the same area as for apseudids (Fig. 2 B, C).

The ski-pole arrangement with the dactylus spine is developed in all species described in the literature of both groups (perhaps with the exception of the aberrant genera Venusticrus and Carololangia of Neotanaidae (GARDINER, 1975)). The slender, filiform uropods composed of numerous short articulations is another common characteristic, like the antennulae, with the strongly developed and attenuated peduncle. The flagellum is more articulated in Apseudes than in Neotanaeis, maybe due to the former's broader cephalosome. Neotanaeis has a narrower cephalosome and more slender body. In both cases, the two pairs of antenna are just long and slender enough to function as tactile sense organs in soft-sediment tubes (Figs. 1, 3).



Fig. 3.

Apsseudes spinosus in their tubes (horizontal section), showing the ski-pole arrangement of PIII-PVII, where dactylus acts as pole and the propodal and carpal setae as the discs. When tunneling a new tube, the old is closed off by a wall of larger fragments, a brick by brick procedure.

A prerequisite for tube-dwellers is the ability to turn inside the tube (JOHNSON and ATTRAMADAL, 1982a), otherwise they would be more often exposed to predators. In A. spinosus, tunneling results in a tube, often elliptical in cross-section and almost twice as broad as the body laterally, with the narrow diameter dorsoventrally. Turning is therefore executed sideways, lying on its side, the pleon is bent ventrally towards the head and the movement is continued with the help of PV-PVII until the head is raised in the opposite direction. The flexible uropods bend easily and are kept dorsally on the pleon during the turning.

The form and size of the tubes generally follow the topography of the sediment, and shells or smaller stones are taken advantage of as 'roof'-armaments. The result is more or less winding tunnels with an approximate length of 5 to 10 times the body length. This varied among individuals and instars, and depended on the age of the tube. The tube always had two openings recognizable on the surface as small funnels (Fig. 1), and sometimes marked by the owner's excuviae remnants. Now and then old tubes were changed or renovated by making a new tube and closing off most of the old. The closing-off is a brick by brick procedure, a cheliped picking larger fragments from one side of the tube wall and putting them down in front of the other cheliped which lays the fragment into the wall (Fig. 3).

Feeding

Analysis of the stomach content did not reveal any identifiable remains except for fine sediment particles. A. spinosus is a deposit feeder, eating from the floor and sides of the inner tube. When a tube area was cleaned of finer sediment and mainly gravel and coarse sand particles remained, new sediment was obtained outside the front-opening, from an area which could be reached without completely vacating the tube. This behaviour resembles that of Tanais cavolinii (Milne-Edwards) (JOHNSON and ATTRAMADAL, 1982a). It is a rapid venture, which involves embracing the largest possible amount of sediment between the chelipeds and the front head, followed by a fast retreat into the tube. The sediment is then trampled and packed into the tube wall.

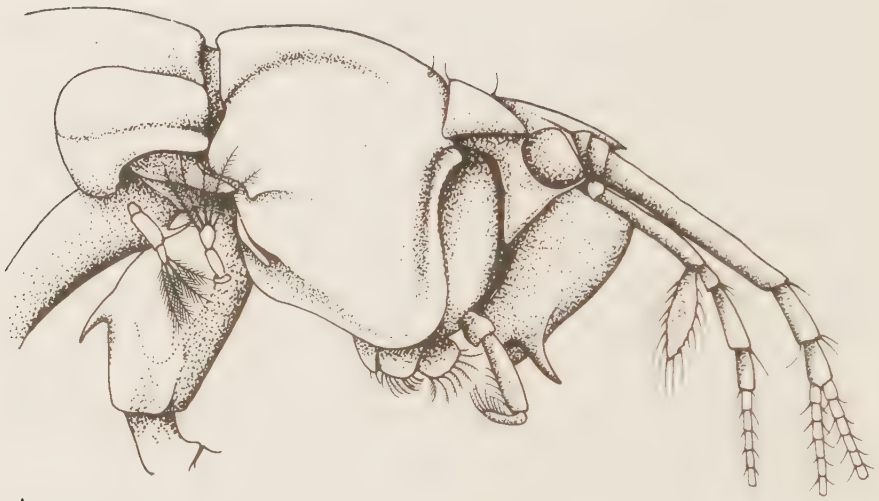
A. spinosus feeds in the same way as T. cavolinii, picking up sediment with the chelipeds and transferring it to the maxillipedal palps, which convey it to the mouthparts. The propodal 'finger' of the cheliped has a corresponding armament of small setae, by which fine sediment can be obtained. All instars use the chelipeds in the same way, even the copulatory males which have enlarged chelipeds (sexual dimorphism). The contents of several guts of Neotanaeis were examined by GARDINER (1975). The contents were consistently composed of formless material, presumably organic detritus, and occasional fragments recognizable as "having had a biological origin". No structure on the mouth parts or elsewhere indicates that Apseudes or Neotanaeis have a special mode of feeding as filter-feeders (as was suggested for A. talpa by DENNEL, 1937),

scavengers or carnivores. In Neotanais, the chelipeds are somewhat shorter and stouter than in Apseudes, but the chelae show a resemblance in shape, cutting edge and setation. (An exception is the N. hastiger group of species which have a fist-shaped chela and rounded teeth instead of cutting edges.) Although many of the differentiations in cheliped structures may reflect various adaptations to food resources and to cutting and crushing, they are used as an allround device for feeding, burrowing and defence etc. (sexual dimorphism of the male's cheliped, excluded).

Respiration and pleopod pumping

The respiratory chambers are enclosed in the lateral carapace lobes, and respiratory currents are produced by the maxillipedal epipodites. Each chamber has two openings, one ventral pore and one lateral pore, at the posterior margin of the carapace. In front of the latter pore through which the respiratory water enters the chamber, are two exopodites, one borne on the basis of the cheliped and one on the IInd pereopod (Fig. 4 A), with feathered setae which overlap. These can be kept tight over the pore when burrowing but are generally seen pumping towards the pore.

In addition, the branchial cavity of apseudids may be protected on the interior by the maxillipedal epipodite (epignath) which has an extra moveable lobus with fine hair (Fig. 4 B). This may have the function of cleaning and sealing off the respiratory pore.



A



B



C

Fig. 4.

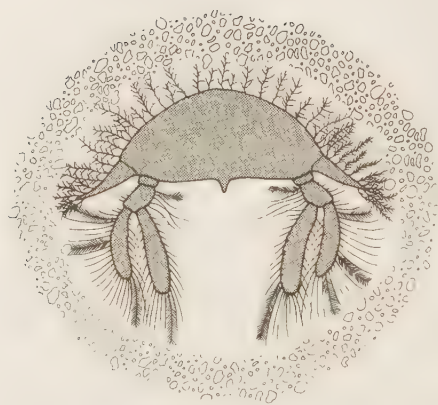
- A. *Aapseudes spinosus*. The two feathered exopodites, on basis of the cheliped and the IInd pereopod, assist respiration and prevent the lateral respiratory pore from fouling.
- B. *Aapseudes spinosus*. Maxillipedal epipodite (epignath), with an extra moveable lobus with fine hair developed.
- C. *Neotanaïs*. The bi-lobus epipodite distally curved with a brush of fine setae.

In neotanaids which lack rudimentary exopodites, the respiratory pores are also laterally situated but are attenuated in oblique furrows between the border of the carapace and chelipedal coxa (Pl. II, A), a location which protects against fouling from fine sediment particles. In addition, a very close lattice-work (Pl. II, B) covers the pores. The bi-lobus epipodite (epignath) has a curved distal part with a terminal brush of fine setae (Fig. 4 C). This has the same function as the additional lobus in Apseudes, sealing off the pores from the cavity, and functioning as a cleaning device with the aid of the fine setae (Pl. II, C).

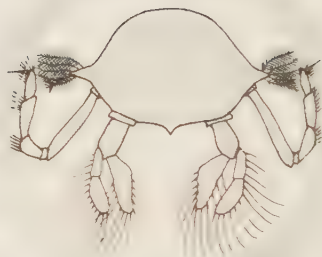
A third pumping activity is carried out by the pleopods. The five pairs are well developed with long and slender feathered setae, by which a smooth water current is generated through the tube. They perform a slow and intermittent metachronal rhythm with a short beat amplitude. This is similar to T. cavolinii (JOHNSON and ATTRAMADAL 1982a), and results in a one-way water current.

A caudal view of a tanaid pleopod (Fig. 5) shows the exopods and endopods, which are spread like a fan during the power stroke with the fringe of pleopodal bristles curved. The semicircle of the pleopods and the semicircular body make a complete circle in cross-section, reflecting the form of most tubes.

The pleon is narrow with the five segments somewhat reduced with well developed spiniform projections densely clothed with long, feathered bristles. The bristles are also well developed on the last pereopods (PVII). The posterior part of the body is consequently always thickly covered with mud



A



B

Fig. 5.

- A. *Aapseudes spinosus* in its tube (cross-section, caudal view). The spiniform projections and long feathered setae on the pleon are embedded in mud and function in sealing off the semicircular area of the tube dorsolaterally. The fringe of pleopodal bristles is curved.
- B. *Neotanaïs* in its tube (cross-section, caudal view). Groups of certain species are equipped with sealing arrangements laterally on each pleonite, similar to *Aapseudes spinosus*, and sometimes with more or less developed spiniform projections. The fringe of pleopodal bristles is curved.

adhering to the spiniform projections and to the many setae and bristles. In this way the pleon equals the size of the pereon. It has its function in sealing off the semicircular area of the tube dorsolaterally, and together with the seal on PVII prevents recirculation of water, improving the efficiency of the one-way pumping system by canalizing water to a ventral groove (Fig.5 A).

Most neotanaids have developed similar arrangements with some variations in the furnishment of setae on the pleons. The species groups americanus, pfaffi and hastiger (GARDINER, 1975) are equipped with such arrangements laterally on each pleonite, sometimes with more or less developed projections (Fig. 5B). This is also characteristic of N. calcarulus, N. barfoedi, N. insolitus and the monotypic genera Venusticrus and Carololangia (GARDINER, 1975). N. calcarulus has a somewhat shorter pleon with feathered bristles originating from the fringe of the pleonites, which are lateroventrally directed. As the posterior pereopods have an additional lateral sealing function, they are furnished with richly developed setae, similar to the last pereopod of A. spinosus.

As more or less irregular tunnels obstruct this mechanism, the specimens were observed favouring one or two narrower sites in the tube when ventilating (Fig. 3). Ventilating could also be improved by the posterior part of the body being positioned around a corner, or by the animal lying on its side (Fig. 3).

4. DISCUSSION — with a comparative analysis of

Apseudidae and Neotanaidae

Tanaid crustaceans are well represented with abundant deep-sea species, some of which are found in the hadal zone, inhabiting depths exceeding 8000 m (GARDINER, 1975; LANG, 1968; WOLFF, 1956). The deep-sea Tanaidacea are mostly confined to two groups, the neotanaids (Dikonophora) and the apseudids (Monokonophora). The genus Neotanaïs is best represented, having more than 25 species (GARDINER, 1975). Including the monotypic genus Herpotanaïs of the same family, it represents by far the largest species, measuring from 5 mm to 25 mm, and according to WOLFF (1956), is "one of the most abyssohadal families or larger taxons of marine invertebrates to be found". The average vertical distribution of the genus Neotanaïs is 3000-8000 m, and it is almost cosmopolitical, excluding the Norwegian Sea and arctic regions.

The other group, the apseudids, is less confined to the deep-sea than the former, but the genera Apseudes and Sphyrapus are characteristic for deeper coastal waters, fiords and the deep-basins in the Norwegian Sea. The deepest record is 6800 m (WOLFF, 1956). Apseudes and Sphyrapus are common in high latitudes (boreal and arctic regions), where Neotanaïs is missing.

Most neotanaid and apseudid material comes from various deep-sea expeditions, and has been used primarily for systematic work. Thus, knowledge of their role in deep-sea benthic communities is very limited. The systematics, postmarsupial development and distribution of Neotanaidae are treated in a

comprehensive work by GARDINER (1975). Other phenomena described for deep-sea species of Neotanais and Apseudes are hermaphroditism (LANG, 1953, 1958; WOLFF, 1956), and size frequency and vertical distributions (WOLFF, 1956). With this investigation of A. spinosus, the connection between form and function of deep-sea Tanaidacea has been brought into perspective with its proper background, for the first time.

Apseudes spinosus agrees well with the functional model of the tube-dwelling tanaid T. cavolinii (JOHNSON and ATTRAMADAL 1982a) with regard to joints and articles of the pereopods, and the location of spines and setae. An inverted position of pereopods III-VII is characteristic for tube-dwellers, e.g. for the tube-spinning species of Tanais (JOHNSON and ATTRAMADAL, 1982a), Heterotanais (BÜCKLE-RAMIREZ, 1965), Typhlotanais, Leptognathia (GREVE 1967), as well as for the tube-tunneling tanaid A. spinosus in this report. The legs of Neotanais also fit this pattern (Pl. I D, I I D). GARDINER (1975) suggests that the neotanaids have adapted to free-walking on top of the sediment, because of the absence of developed "fossorial limbs" such as those found in Apseudes or Sphyrapus, but in my opinion this is not a convincing argument.

For A. spinosus, tunneling in the sediment involves the antennulae, chelipeds, IInd pereopods and all the other legs. Tunneling would not have been possible with only the "fossorial limbs". "Fossorial limbs" is therefore not a term to be used only for the IInd pereopods, which were given this

name because of their deviating shape. Strongly developed spines and the broad, flattened propodus have the important function of protecting the antenna and preparing a preliminary path for the tunneling work clearing the way of gravel and coarse sediment with their saw and pitch-fork action. The stout bordering spines of the IInd pereopod facilitate tunneling in mud intermingled with stones and gravel, and therefore can be regarded as an adaptation for tunneling in this sort of sediment. Such sediments are common along the slopes in fiords and coastal waters, but unusual in the deep-sea, except for the Arctic where such material is brought about by drifting ice and it is also in this area that tanaid species with most pronounced 'fossorial limbs' are common, e.g. Sphyrapus serratus (Pl. II, E). In Neotanais, which is not represented in the Arctic, all pereopods are more uniform and the IInd pereopod is not so 'fossorially' accentuated, having long bristles instead of stout spines (Fig. 2 C). Yet, this probably functions analogously in homogeneous soft sediment where long bristles suffer no chance of being broken by coarse particles. However, in species found in the North Atlantic close to coastal, boreal or glacial areas and in the Antarctic (e.g. N. americanus, N. affinis and N. antarcticus), as well as in other widely distributed species, e.g. N. sandersi, N. hadalis, N. laevispinosus, and N. peculiaris, the carpal and propodal setae of the IInd pereopod are developed into stout spines (Fig. 2 B). Independent of whether spines or bristles are developed, about the same area is covered. This might be a homologous adaptation to the 'fossorial' IInd pereopod of Apseudes and Sphyrapus, resulting from a variation in the sediment structure.

The small rudimentary exopodites present only in monokonophoran tanaids on the bases of the chelipeds and IInd pereopods, have a protective and assistant function in the respiration of A. spinosus. To prevent the respiratory pores from fouling when burrowing, the pores are located laterally (not dorsally as in Tanaidae), and are protected exteriorly by the feathered setae of the exopodites. Interiorly, the bi-lobus epipodite may clean and seal off the respiratory chamber.

In neotanaids, rudimentary exopodites are missing, and the elongated furrows which are respiratory pores are protected from fouling exteriorly by the close lattice-work, and interiorly by the terminal brush of fine setae on the epipodite.

Pleopods are well developed in both apseudids and neotanaids. In general, male pleopods are comparatively larger, with more numerous and longer setae. In experiments with A. spinosus, no instars were willing to swim and I do not believe they can. Still, I cannot see any other reason why the male has more developed pleopods, which is a general phenomenon among tanaids. In the dense population from which the specimen of A. spinosus was obtained, it would not be necessary to swim to find copulatory females. However, in less dense populations of deep-sea species, an ability to swim would perhaps be favourable. In A. spinosus, the pleopods were never used when 'walking' on the substrate. If neotanaids were "epifaunal, spending their lives on the surface of the deep ocean oozes" (GARDINER, 1975), there

would be no use for pleopods. Tanaids are not built as swimmers, which means that if or when they swim, it is an occasional and probably perilous event. Pleopods in tanaids are not respiratory organs, but are generally developed for ventilation and for assisting respiration (JOHNSON and ATTRAMADAL, 1982a). Pleopods of female tanaids are not developed as natatory pleopods as they are in other peracaridan groups (Isopoda and certain Mysidacea).

To increase pumping efficiency by producing a one-way waterflow through the tube, A. spinosus has developed spiniform projections laterally on the pleonites, which are densely clothed with long, feathered bristles.

Neotanaids also have homologous structures, but these seal off the lateral sides preventing lateral and dorsal backflow, and indicate predictably smooth and regular tubes in cross-section.

The structural plan of A. spinosus is well adapted to the physical properties effecting a tubicolous life-strategy. Several morphological characteristics are shared with T. cavolinii, reflecting a parallel development of solutions to the same problem. On the other hand, several morphological characters distinguish the two species, as a result of the different kinds of environment they inhabit. A comparison of Apseudes and the deep-sea taxon, Neotanais, reveals an affinity in most functional characteristics, and indicates similar adaptations as those described for A. spinosus.

It follows therefore that neotanaids have evolved a similar tube-dwelling strategy to the apseudids. Certain morphological differentiations (e.g. in the 'fossorial' IInd pereopod and in respiratory pores) can be the result of differing kinds of substrate, such as fine deep-sea sediment as opposed to sediment intermingled with shells and gravel.

The large amount of common characters within the two phylogenetic lines, Neotanaidae and Apseudidae, must have arisen through convergent and/or parallel development. Many of the characters described and discussed above, are adaptations to similar abiotic environmental conditions, for tunneling and for tube-dwelling habits. An evaluation of taxonomic characters must therefore be considered in the light of these facts.

The world-wide distribution of the neotanaids includes several records from highly boreal areas of the North Atlantic, e.g. N. americanus, a species which is also reported from Antarctic waters as shallow as 500 m (GARDINER, 1975). Although many deep-water organisms are elevated at high latitudes (EKMAN, 1953), the question of what has stopped the neotanaids from colonizing the deep basins of the Norwegian Sea and the Arctic comes to the fore. I suggest three possible causes:

- 1) This archaic deep-sea family has never managed to overcome the shallower, rocky ridges surrounding and isolating the deep basins of the Norwegian Sea.
- 2) It was once widely spread in this region but became extinct together with many other faunal elements during periods of drastic climatic changes. The subsequent invading fauna has hitherto mostly been recruited from

shallower areas, e.g. the apseudids. 3) This family is stenotopically adapted to soft deep-sea sediment free of coarse particles and gravel.

To answer this more completely, and to further improve our understanding of the biology of deep-sea tanaids, there is a pressing need for live observations of their functional morphology and experimental studies of living specimens from the deep-sea.

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- Plate I (A-C) *Apseudes spinosus*.
A, pereopods PVI and PVII, propodus and dactyli (X90)
B, distal part of propodus on PIV (X240).
C, the same soft feathered setae (X1200).
(D) *Neotanaïs*. 'Ski-pole disc' setation of carpus on
PV (X180).
- Plate II (A-C) *Neotanaïs*. A, the respiratory pore, attenuated in
oblique furrow between the border of the carapace
and chelipedal coxa (X24). B, a very close lattice-
work covers the pore (X240). C, the lattice-work
through which the fine setae of the distal epipodite
appear (X1200).
(D) *Neotanaïs*, pereopods in rostral view, showing the
V-form position (X60).
(E) *Sphyrapus serratus*, IInd pereopod (lateral view, X90).

Plate I

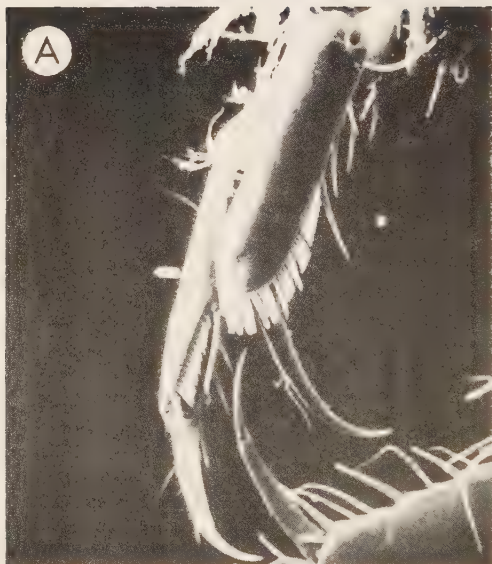
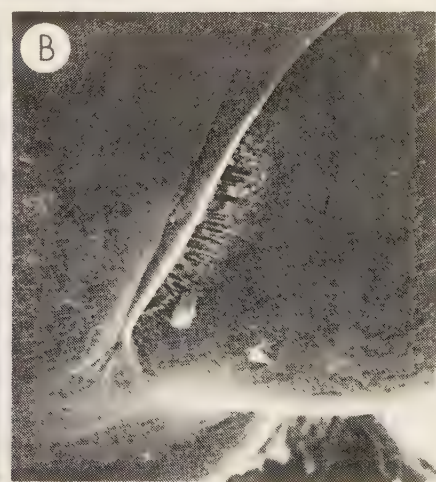


Plate II



A SIMPLE PROTECTIVE COD-END FOR RECOVERING LIVE SPECIMENS

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Abstract: A protective cod-end mainly for use on sledges for the recovery of living animal specimens from any depth, is described. It operates independently of surface signals. Mechanical damage of the specimens is avoided and also exposure to bathymetric fluctuations of salinity, temperature and light during recovery. The device has been tested on benthic and hyperbenthic fauna at varying depths down to 700 m.

INTRODUCTION

Research on the biology of living animals is dependent on an ability to recover successfully intact living specimens from their natural habitat. Benthic organisms in general, and stenotopic deep living species in particular, are sensitive to changes in environmental conditions and therefore must be protected from exposure to bathymetric fluctuations in salinity, temperature and light. The rapid changes in the light intensity and light quality from depths as small as 30 m may irreversibly degenerate eye-structure (Loew, 1976). Crustaceans subjected to the traditional recovery procedure have been noted to display abnormal behaviour. Rapid thermal and osmotic changes, and a combination of both factors, are either lethal, or affect the animals to an extent that hampers histological analyses, behavioural studies, and studies of their functional morphology. More fragile specimens, such as several crustaceans, suffer severe mechanical damage in unprotective cod-ends. Protective cod-ends for the recovery of deep-living midwater animals has been designed and used satisfactorily by Childress *et al.* (1978). Our investigations of benthic and hyperbenthic crustaceans living at various depths led to the following requirements for a protective cod-end.

- (1) Economical construction.
- (2) Ability to fit into different gear-types, and to operate automatically, independent of depth.
- (3) Simple design with no sensitive mechanical devices, as reliability is essential for expensive deep-sea sampling programs.
- (4) Minimal changes in temperature and salinity during recovery.
- (5) Provide protection against light exposure.
- (6) Minimal mechanical damage of specimens.

DESIGN, CONSTRUCTION AND PERFORMANCE

The cod-end is made of dark coloured opaque polyvinylchloride (PVC), which is readily available, easy to work with and has been successfully used for similar cod-ends (Childress *et al.*, 1978). The design is shown in Fig. 1. The cod-end consists of a piece

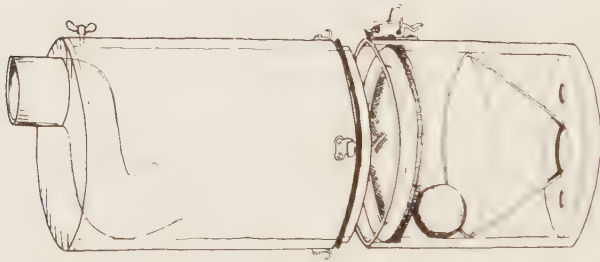


Fig. 1. The two sections of the cod-end showing internal parts, with a Z-formed tube acting as a light barrier.

of PVC tube with an opening at each end. The tube is divided so that the cod-end can be deployed in two halves, which are sealed by an O-ring and kept together by four stainless-steel release clips. A filtering net which can easily be exchanged for nets with varying mesh-sizes, is placed between the two halves to retain the catch. In the back section of the cod-end a spherical weight, enclosed in a funnel, acts as a valve. When the cod-end is placed in an approximately vertical position, the weight rolls down and seals the back opening (Fig. 3A). When the cod-end is placed in a more horizontal position, the weight rolls away from the opening (Figs. 1, 3B).

COD-END FOR LIVE SPECIMENS

The device is securely attached to the rear end of a traditional benthic gear, such as a sledge or trawl. From the trawl net the water enters the front section of the cod-end through a dark coloured tube which acts as a light barrier and prevents light-reflexion. A looped piece of flexible hose (Fig. 2) and a Z-formed PVC tube (Fig. 1) were tested as light barriers. The front opening can be adapted according to animal size, but it should have a larger diameter than the back opening to reduce the velocity as the

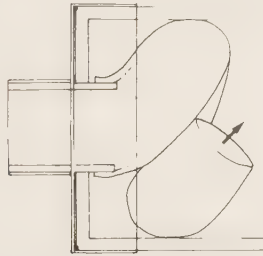


Fig. 2. An alternative light barrier made by a looped flexible hose.

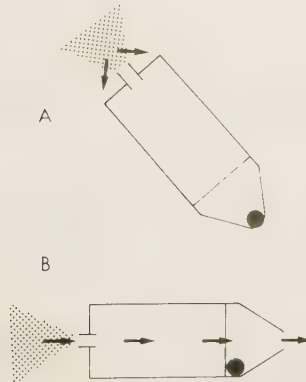


Fig. 3. A, position of the cod-end when the gear is retrieved or lowered; the valve is closed by the spherical weight; B, sampling position of the cod-end, when the gear slides along the benthos; the valve is open and allows the through-flow of water.

animals pass through the light barrier tube and enter the front section of the cod-end. We have used front openings with diameters ranging from 5 to 7 cm, and corresponding back openings of 4 to 5 cm. The catch is retained in the front section between the light barrier tube and the circular net.

The total length of the cod-end described here, 50 cm (30 + 20), is the average length most suitable for our gear-types. The external diameter is 22.5 cm, the internal diameter $\approx$ 20 cm. A thick tube wall of $\approx$ 1.3 cm is needed as the connecting two halves must be lathed, leaving an overlap of $\approx$ 5–6 mm, which is then sealed by an O-ring 2 mm in diameter. The filter consists of a planktonic net glued between two rings of PVC, 5 mm in diameter. When the two sections of the cod-end are connected by the release clips, the filter is tightly squeezed and kept in place. The clips should be positioned as in Fig. 1, because if oppositely oriented, the loops of the clips tend to hook themselves, making it difficult to disconnect the two sections.

A vital part of the cod-end is the closing mechanism at the rear. In Fig. 1, the opening is 5.2 cm and the spherical weight has a diameter of 5.8 cm. The opening is edged with a seal of the type used for sealing windows, and the heavy weight of the sphere against this keeps the cod-end water-tight. The weight is made of stainless acid-proof steel. The cod-end should be aligned with the gear. During lowering and retrieving, the gear hangs from the wire at an angle that ensures that the cod-end is sealed (Fig. 3A). It should not, therefore, be towed at great speed. The weight is not released from the funnel opening to allow the through flow of water, until the gear slides along the bottom (Fig. 3B).

The cod-end has been used with a modified Beyer epibenthic sledge (Oug, 1977), and a similar sledge with both a hyperbenthic and a benthic net. The cod-end proved effective for the recovery of living crustaceans from deep Norwegian fjords, and from the slopes of the Norwegian part of the Barents Sea, areas with distinct salinity and temperature stratification.

The cod-end fastened to a hyperbenthic net performed well, and there was no leakage, but the cod-end on the benthic net leaked slightly when full of mud. To prevent clogging and malfunction, relatively short hauls are recommended when operating in soft sediments.

The ability to keep the salinity constant is dependent on the reliability of the closing valve. The cod-end was tested twice in water with a salinity of 34.9‰ at the bottom (230 m), 30.1‰ at 20 m depth, and $\approx$ 28‰ at the surface. For the first test, the cod-end was filled with surface water of 27.8‰ and hauled for 5 min. The water in the cod-end then had 0.8‰ lower salinity than the bottom water of 34.9‰. For the second test, the cod-end was filled with water of $\approx$ 34‰ and hauled for 15 min. The salinity of the water in the cod-end was now identical to that of the bottom water (34.9‰). The cod-end was water-tight on both occasions, but to ensure constant bottom water salinity inside the cod-end, it is necessary to haul for a longer period or to fill the cod-end with bottom water before lowering it.

If the cod-end is made of PVC, like the ones used by Childress *et al.* (1978), we can

COD-END FOR LIVE SPECIMENS

assume that the temperature insulation is adequate, but if better insulation is required, we suggest an additional outer layer of neoprene, which helps prevent excessive heating in the top 50 m and on deck.

Sampling with a protective cod-end resulted in very little mechanical damage, even to very fragile organisms such as the mysids *Boreomysis megalops* G.O. Sars and *Erythrops serrata* (G.O. Sars) and other delicate crustaceans. Also, the specimens recovered with a protective cod-end and later kept in aquaria, had a low mortality compared with those sampled with ordinary cod-ends (Jan Helge Fosså, pers. comm.).

If it is essential that the front opening be kept closed during the recovery, we suggest that a closing valve be used in the same way as the seal at the back opening (Fig. 4). In this case the light barrier tube is superfluous.

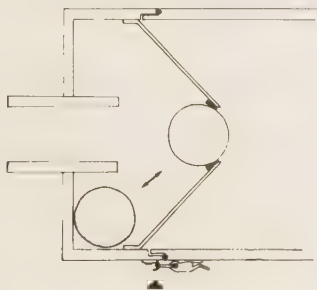


Fig. 4. Additional closing valve at the front opening of the cod-end; note that the connection point is here placed close to the front.

If a great density of specimens is collected in one haul, they should immediately be transferred to a greater volume of water of similar quality, to ensure low mortality during transportation.

As the closing mechanism of this cod-end is very simple and reliable, it can probably easily be adapted to suit various needs, e.g. it could be fitted onto other types of cod-ends, traps, water samplers, etc.

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A FUNCTIONAL-MORPHOLOGICAL MODEL OF TUBE-DWELLING
TANAIDACEA (CRUSTACEA)

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ABSTRACT

The morphology of the body-form, legs and appendages in Tanaidacea is uniform, following a few general patterns, which have been simplified into a tanaid model. The degree of abiotic impact on various structures in differing environments can be distinguished, and thus separated from or evaluated with characters of phylogenetic value. Most of tanaidacean taxa can be divided into two hypothetical guilds, tube-spinning forms and tube-tunneling forms. These can further be subdivided considering the nature of the tube, its permeability, the substrate of the habitat, and the size of the species. Different taxa have acquired several morphological features in common, as a result of adaptation to a tube which is more or less circular in cross-section. All legs are developed for inverted (V-form) position. The fringes of the pleopodal exopodites and their bristles are curved in alliance with the tube wall. Each pleopod pair covers a semi-circular area in the tube. The size, form, and number of pleonites, fusions or reductions, depend on the type of sealing arrangement on pleon, which is a consequence of the permeability of the tube, except for the smallest species where pleopods are superfluous.

INTRODUCTION

The tube-dwelling habit is a scattered phenomenon among crustaceans and a well-developed strategy for several peracaridan malacostracans. The order Tanaidacea has a generally uniform pattern in the morphology of body form, legs and appendages (with some exceptions, e.g. *Tanzanapseudidae*, M. Bacescu, 1975). Reports on primarily *Tanais cavolinii* (Milne-Edwards) and *Apseudes spinosus* (M. Sars), describe this phenomenon as a functional adaptation to tube-dwelling (Johnson and Attramadal, 1982a; Johnson, 1982). It can therefore be presumed that tube-dwelling is a common feature among Tanaidacea. The taxa and functional clusters of species (guilds), from tunneling deep-sea forms to tube-spinning tidal hard-bottom forms, present a limited number of morphological solutions. Some of these are common to all, and some are significant in distinguishing a few main guilds. Different solutions of fundamental problems such as locomotion and respiration have been developed and favoured as a result of different environmental conditions (especially concerning substrate). In this paper, different taxa are discussed in the light of common characters which indicate adaptation to a tube which is more or less circular in cross-section. Further, the characters distinguishing certain guilds are compared and discussed with reference to locomotion and ventilation inside tubes constructed of different substrates.

MATERIAL AND METHODS

Samples of Tanais cavolinii (Milne-Edwards) and Apseudes spinosus (M. Sars) refer to Johnson and Attramadal, 1982a and Johnson, 1982, respectively. Leptognathia breviremis (Lilljeborg), L. gracilis (Krøyer), Typhlotanais tenuicornis (G. O. Sars) were obtained from various stations in the Barents Sea during the 'Ymer 80 Marine Benthos Program (Norvarg)'. The specimens were retrieved alive with the use of a protective cod-end (Johnson and Attramadal, 1982b) attached to an epibenthic sledge. The material was studied on board. Specimens of the genus Neotanais were obtained during the 'INCAL' expedition, at station 8 (55°01'N, 12°32'W). Here, no live material was obtained, and all specimens were preserved in 4% neutralized formaldehyde. Other species refer to the literature cited.

To investigate the exoskeleton some specimens were treated according to a method described by Hessler (1964) which dissolves the soft tissue and calcium of the exoskeleton, using KOH. Thereafter the exoskeleton is stained in the last part of Mallorys triple stain.

TERMINOLOGY

The nomenclature applied to body segments and appendages refers to Wolff (1956:188, 1962:15). The first thoracic somite bearing the maxillipeds and the second bearing the

chelipeds are fused to the head. The third to the eighth thoracic somites bearing the pereopods II-VII are named pereonites 3-8, and collectively referred to as the pereon. The abdomen is named the pleon, and its five free somites, pleonites. The sixth somite is fused to the telson to form the pleotelson. The latter bears the uropods and the pleonites each bears a pair of pleopods.

RESULTS AND DISCUSSION

The tanaids can be divided as tube-dwellers into two general guilds: tube-spinning and tube-tunneling forms. Most of the monokonophoran families and the dikonophoran neotanaids are tube-tunnelers, and the other tanaid taxa can be grouped as tube-spinners.

Tube-dwelling is reflected in the body-form and by various adaptations for facilitating the function of:

2) Locomotion. Forward and backward movements and turning inside the tube (Johnson and Attramadal, 1982a; Johnson, 1982).

2) Ventilation of the tube by means of pleopod pumping (Johnson and Attramadal, 1982a; Johnson, 1982) prevents stagnant water conditions, harmful to respiration and to the brood.

1) LOCOMOTION: BODY-FORM (cross-section view)

The tube diameter conforms to body shape and allows for turning inside by ventral bending. Therefore, the body occupies less than half of the tube diameter (Fig. 1A). The dorsal curvature of the somites conforms to the curve of the tube-wall, utilizing optimum space. The ventral (sternal) area of the body is more or less flattened. In mature females, however, this area could be convexly expanded by the increasing volume of eggs developing in the ovaries, or it could be invaginated by the marsupium, e.g. Heterotanaïs oerstedii (Bückle-Ramirez, 1965). For spatial reasons the pereonites are cut off laterally (Fig. 1 A).

BODY-FORM (longitudinal view)

Locomotion and ventral bending of the body is facilitated by flexible elastic integuments and flexible joints, which are connected dorsolaterally and overlap the somites on the dorsal and ventral sides (Fig. 1B). In addition, some of the spun tubes have a certain elasticity (Johnson and Attramadal, 1982a). The tube diameter of Apseudes spinosus (Fig. 1C) could often be more elliptical, favouring sideways turning. For turning, no somite can be longer than the tube diameter. Also, shorter somites imply less tension on joints and integuments. With a defined tube diameter and a fixed number of segments, the only way to maximize the size of the body would be to increase the length of the somites. Therefore, certain somites have been given priority, while others are shortened.

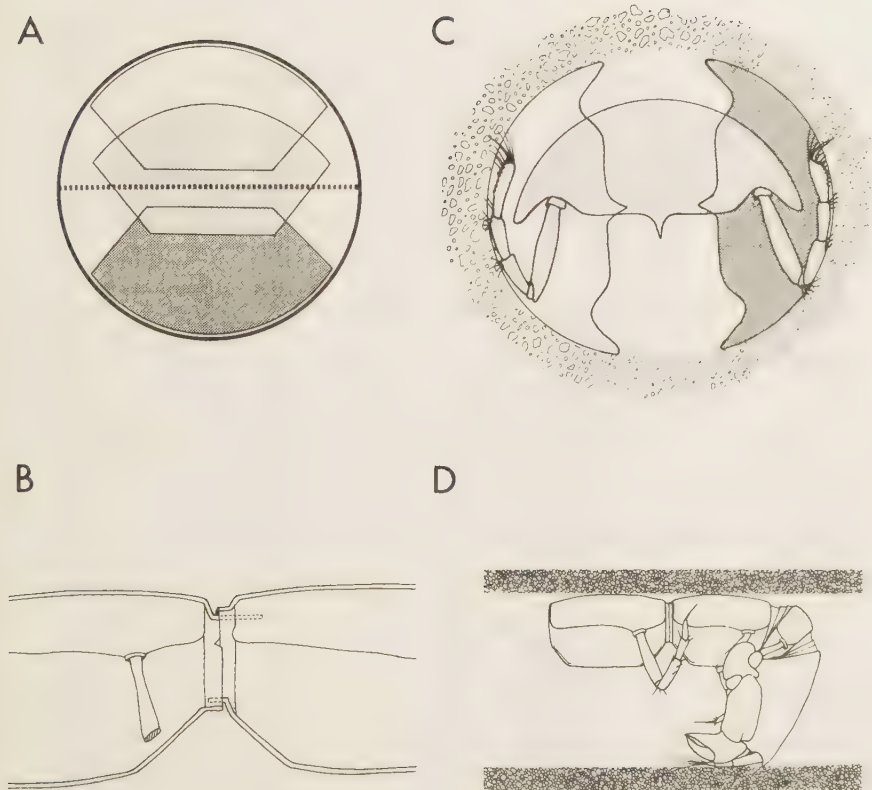


Fig. 1.

- A. Cross-section view of a hypothetical tanaid in its tube. The somites occupy less than half of the tube diameter, in order not to hamper the turning ability. Dorsal curvature is shaped in alliance with the curve of the tube-wall, utilizing an optimum of space. Grey area — 'normal' position, white and dark area — turning. Pereonites are laterally cut off, spacing the pereopods.
- B. Longitudinal section of pereonites. Flexible joints and elastical integument maximize the ventral bending ability.
- C. Cross-section view of *Aapseudes spinosus* in its tube. Grey area indicates normal position of the animal, white and dark areas show turning sideways.
- D. Lateral view of initial turning position. A shortening of the pereonite adjoining the large cephalic segment is a prerequisite for turning ability.

For example, the cephalon is larger as many vital organs and functions are concentrated in this region (e.g. sensory organs, respiration, alimentation etc.). This is compensated for by a shortening of the first free thoracic somite (pereonite 3) (Fig. 1D), a compromise which is a prerequisite for bending the anterior body enough to be able to turn. The cephalon at the front end and the pleotelson at the rear, are favoured in size as they are terminal segments adjoined to only one somite. These segments, together with the central pereonites 5-6 (7), are generally the largest. Maximized pereonites have the advantage of increasing the space for the development of eggs in the ovaries and embryos in the marsupium (Fig. 2), and the adjoined somites must therefore be short so that turning is not hampered.

Walking

The walking legs (PIII-VII) are uniformly developed, often short and stout in tube-spinning forms and somewhat longer and slender in tunneling forms. Joints and articulations are developed for a V-form position and for maximum sensitivity to and contact with the curved tube wall (Johnson and Attramadal, 1982a; Johnson, 1982). The articulations are terminally furnished in tube-spinners with stout spines or bristles (Fig. 4 B), or in tube-tunneling forms with slender setae which help create a functioning 'pad' at each joint (Figs. 1 C, 4 A). The chelipeds and pereopods II are borne in close contact with the cephalon, which is ventrolaterally depressed to allow space for the chelipeds. The dactyli of species inhabiting hard-bottom

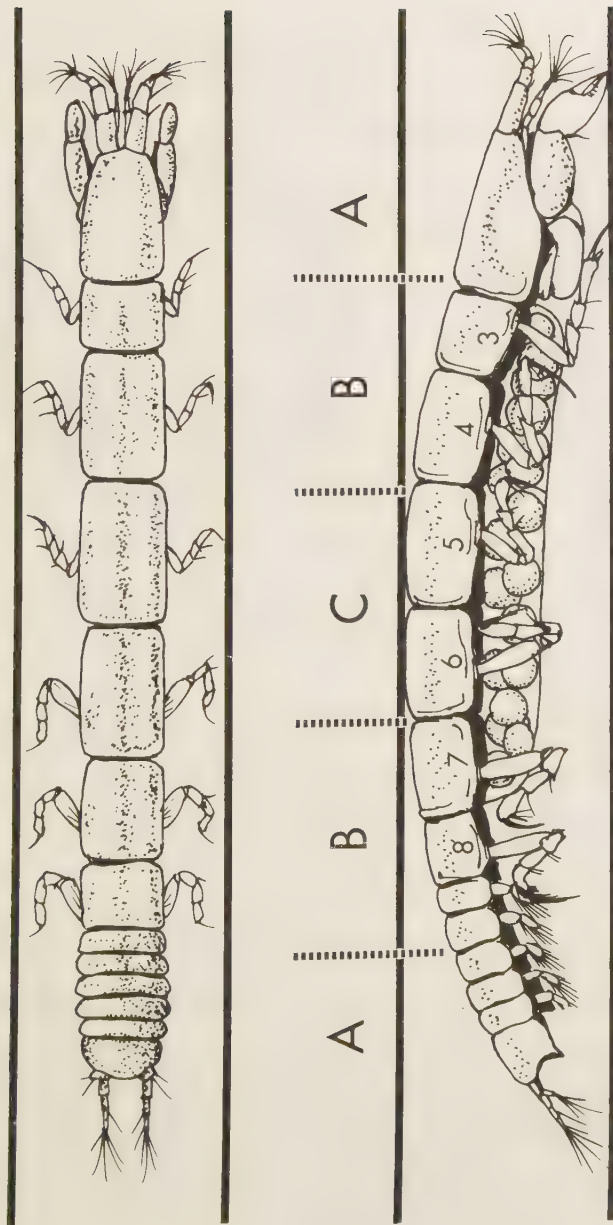


Fig. 2.

Position in the tube (dorsal and lateral view) of a dikontophoran tanaid (*Leptognathia* or *Typhlotanais*), belonging to the category soft-sediment tube-spinners. Increased size of pereonites 5-7 gives more space for development of eggs and embryos. A, B and C are body-portions in different levels of the tube and correspond to the cross-sectioned somites shown in Fig. 3 A.

tubes (e.g. Tanais, Leptocheilia, and Nototanais) are developed as claws on at least the posterior three pairs of pereopods (Figs 3 A, 4 B). In contrast, the dactyli of species living in soft substrate are developed as spines (Apseudes, Neotanais, Leptognathia, Typhlotanais, and Agathotanais), often with fine setae arranged in the form of the disc on a ski-pole, e.g. Apseudes spinosus (Johnson, 1982).

2) Ventilation

Ventilation of the tube by means of pleopod pumping is a more or less continuous procedure (Johnson and Attramadal, 1982a). It is important for respiration as the pumping of the respiratory epipodites in the respiration chambers of the carapace is insufficient for renewal of water in the tube (Johnson and Attramadal, 1982a). Efficient ventilation is also vital for the brood.

Well-developed biramous pleopods furnished with feathered bristles are a common characteristic of most tanaids. Variation is most pronounced among copulatory males, which have extra long and developed pleopods, and among the smallest forms which have reduced pleopods or even lack pleopods. Generally, the pleopods are compactly developed and less natatory (except for copulatory males) in comparison to other peracaridan crustaceans, and it is uncertain whether they are ever used for swimming. As shown in Fig. 3 A, B, the fringes of the exopodites and their bristles are curved to follow the tube wall. Each pleopod pair covers a semicircular area of the ventral space in the tube.

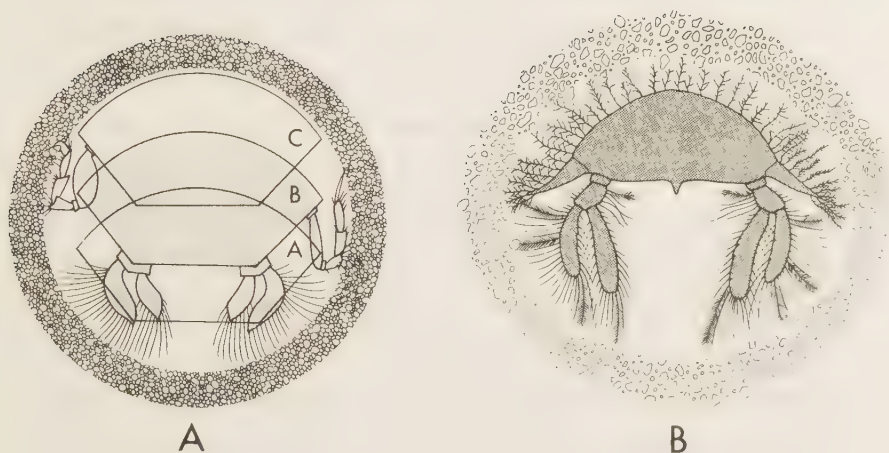


Fig. 3.

Cross-section of the same specimen as in Fig. 2.

- A. Posterior pereonites (C), with tumid pereopods and dactyli developed as claws elevate the body. The resulting contact between the body and the dorsal tube curvature creates a seal against dorsal recirculation of water. The fringes of the exopodites and their bristles (B) are curved in alliance with the tube-wall.
- B. Cross-section of the tube and pleon of *Apsaudeles spinosus*. The curvature of the pleopods follows the somewhat irregular tube-wall. Sealing is facilitated by the pleon being embedded in mud dorsolaterally.

For efficient flow of water metachronal pumping of the pleopods creates a one-way flow through the tube. The water is canalized ventrally by the pleopods, and sealed off dorsally and/or laterally by the pereonites (Fig. 3 A) or by various pleonal arrangements (Figs. 3 B) (Johnson and Attramadal, 1982a; Johnson, 1982). The size, form and number of pleonites, fusions or reductions, depend on the type of sealing arrangement, according to the nature of the tube. The tube wall can be more or less permeable to water depending on the wall construction and/or the substrate enclosing the tube. Two main kinds exist: 1) Tubes made by spinning or tunneling in fine, soft sediment in such a manner that the tube wall is impermeable. 2) Tubes made by spinning on the surface of hard substrates, or by spinning or tunneling in coarse sediment (e.g. sand) or otherwise living interstitially so that the tube wall is permeable.

Impermeable, spun tubes are most common in samples and are also the only presented in the earlier few investigations made on this subject (Bückle-Ramirez, 1965; Greve, 1967). Tubes are constructed in the sediment of fine particles. Sometimes, fecal products are spun together in a web of mucous threads. Fine sediment being trampled and packed by tunneling forms into a tube-wall results in analogously impermeable tubes. Form, size and shape vary with different species and substrates and can easily be confused with tubes belonging to maldanid polychaetes and foraminiferans (Greve, 1967 e.g. Typhlotanais and Leptognathia). The tube-spinners of this group have smooth, dorsally rounded pereonites (cross-section view) which can seal the smooth curvature of the tube

wall when in an elevated position (Figs. 2, 3 A). This is also characteristic for many tunneling forms of this group, among them some species of the deep-sea taxon, Neotanais (suggested as tube-dwellers by Johnson, 1982). Similarly, this is a feature of the more pronounced deep-sea monokonophoran apseudids and the closely related genus, Leiopus (see Lang, 1968 and Wolff, 1956). However, most tunnelers have a characteristically narrow pleon with spiniform projections developed laterally on the pleonites, which are often also clothed with long, feathery setae (Figs. 3 B, 4 A). These setae can be more or less densely developed, and can even cover the pleonite surface and lateral area of pereopod VII (Apseudes spinosus) and/or all the pereonites (Carololangia mirabunda of Neotanaidae). The setae and spiniform projections are naturally embedded with mud, increasing the functional size of the pleon at these sites in its capacity as a soft seal. In Apseudes spinosus, a large seal of mud conceals the whole pleon which becomes semicircular in cross-section (Fig. 3 B), while in Neotanais, the seal is restricted laterally (Fig. 4 A). This difference might be explained by the difference between deep-sea substrate utilized by Neotanais and the substrate from the shallower habitat of Apseudes. More homogeneous and fine deep-sea sediment allows a tube with a smooth and regular inner surface. To seal off the pleopods from backwash it would be sufficient only to have seals developed laterally. In the habitat of Apseudes spinosus, the sediment is intermingled with coarse material such as stones and gravel. The tube is therefore usually winding, with varying diameters and an

irregular inner tube surface, which makes sealing more difficult. This problem is overcome by the whole pleon being capable of sealing corners and narrower stretches of the tube (Johnson, 1982).

The group of permeable tubes has given rise to other problems and solutions. These are most clearly demonstrated by the shallow-water family Tanaidae. Members of the genus, Tanais, spin tubes in association with various algae on hard substrates free of sedimented particles. The tubes are consequently irregular, and varying in diameter. Dorsal and lateral sealing is accomplished by two transverse bands of long, stout and densely feathered bristles on the first two pleonites (Fig. 4 B). Only three pairs of pleopods are developed. These are levelled with the transverse pleonal seals for maximal pumping efficiency, preventing a backflow of water and by their compactness also to minimize the permeable area of the tube wall. A leakage through the network in the pleopod pumping area would result in a decrease in the hydrostatic pressure and a consequent reduction in pumping efficiency. This explains the compact pleon with compact pleonites and the reduction in number of pleonites and pleopods (Johnson and Attramadal, 1982a). This type of reduction has been even further developed among certain species of the dikonophoran tanaiids, where rudimentary (Fig. 5 A) or complete loss (Fig. 5 B) of pleopods is a scattered phenomenon among the different taxa. A common characteristic of these species is their small size and/or narrow body. A disadvantage of this is that the physical properties of water have a stronger effect. The adhesion force

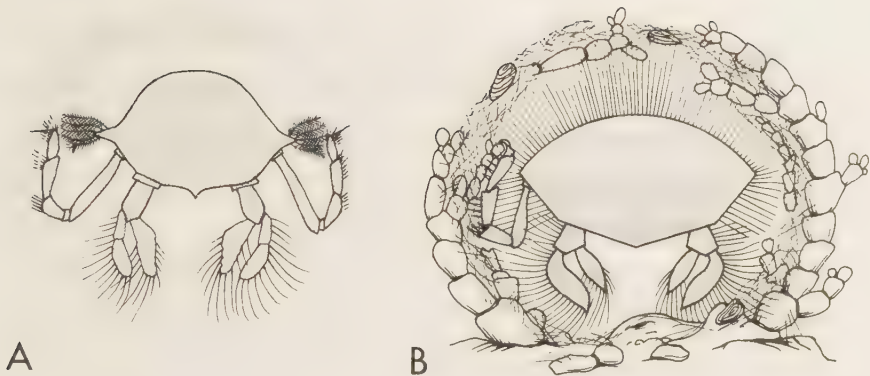


Fig. 4.

- A. Cross-section of the tube and pleon-pereon of *Neotanaïs*, showing the position of legs and pleopods, and the small spiniform projections and feathered setae developed as a lateral seal.
- B. Cross-section of the tube and pereon-pleon of *Tanaïs* in the irregular and permeable tube. A sealing is created by two transverse bands of densely feathered bristles on the first two pleonites. Pereopods have dactyli developed as claws, and the setae of articles are differentiated as spines.

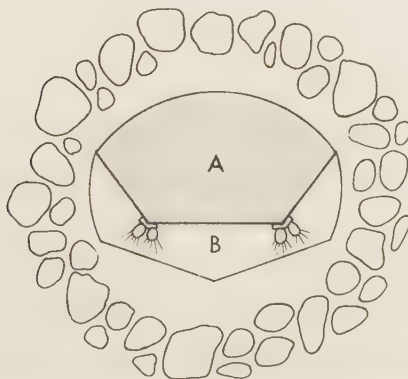


Fig. 5.

Cross-section of two kinds of pleon in a hypothetical tube in comparatively coarse sediment, belonging to the category 'permeable tubes', where the leaking tube wall prevents ventilation of the tube by pleopod pumping.

A. Pleon with rudimentary pleopods (e.g. *Agathotanaidae*).

B. Pleon with complete loss of pleopods (e.g. *Anarthrura* and *Strongylura*).

of water increases proportionately, which means that in tubes with diameters of about 100 μ , creating a through-flow would require comparatively more energy. Also, viscosity increases rapidly when the temperature of sea-water falls below zero. Negative temperatures are not unusual where these species occur. Ventilation of the tube by means of active pleopod pumping might therefore be too difficult or energy demanding. On the other hand, small organisms benefit by having respiration facilitated by diffusion. All these factors may have interacted, with the result of reductions or complete loss of the pleopods in small or slender tanaids. Some of these species inhabit coarser sandy sediments (e.g. Anarthrura), live interstitially or spin their tubes of comparatively larger particles (Fig.5 shows such a hypothetical tube). The leakage through the wall would be considerable, and thus obstructing any longitudinal through-flow of water, preventing ventilation.

This general tanaid model should be regarded as an attempt to simplify the Tanaidacean structural plan in order to distinguish the degree of abiotic impact on different structures in various natural habitats. Most of the Tanaidacean taxa can be referred to one of the hypothetical guilds described above. This improves our understanding of the ecological potential and morphological differentiation within Tanaidacea. Furthermore, various functional solutions are reflected in the convergent or parallel development of certain structures, and this is important for the proper evaluation of taxonomical characters. Analyses and comparisons of similar functional

models constitute a promising approach to the problem of understanding the evolutionary processes which have taken place within higher taxa. The model concept has recently been tested on Crustacea Malacostraca and Amphipoda (Dahl, 1976, 1977) and on Tanaidacea (Tanaidae) (Johnson and Attramadal, 1982a).

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